STRUCTURAL DYNAMICS OF BOREAL FOREST ECOSYSTEMS ON THREE HABITAT TYPES IN THE HONDO - LESSER SLAVE LAKE AREA OF NORTH CENTRAL ALBERTA IN 1983

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ABSTRACT

The primary purpose of the SEADYN Boreal Forest Ecosystem Project is to intensively study and document the short- and long-term structural dynamics of the plant community and environmental components of eight boreal forest ecosystems representing different successional stages on three important habitat types in a clean airshed area of the Southern Boreal Subzone of north central Alberta.

Eight 50 x 50 m reference stands were established and surveyed in the Hondo - Lesser Slave Lake area in 1980, including four stands ranging in age from 42 to 128 years on the *Picea glauca* [*Pinus banksiana*]/*Linnaea borealis* habitat type on aeolian sand; two ranging in age from 73 to 128 years on the *Picea glauca* [*Populus tremuloides*]/*Aralia nudicaulis* h.t. on clay-rich glacial till; and two ranging in age from 62 to 128 years on the *Picea mariana* [*Larix laricina*]/*Ledum groenlandicum* h.t. on peatland.

Five years of intensive, non-disruptive measurements of several important vascular plant and terrestrial bryophyte and lichen population and community parameters began in 1981 and continued in 1982 and 1983. This report describes some of the results obtained during the 1983 snow-free season and compares some of these with results obtained in 1981 and 1982.

In addition to the work already initiated in 1981 or 1982 and continued in 1983, seven new studies were started in 1983, including (1) line-intercept surveys of

plant cover at monthly intervals, (2) assessments of death and decay of dead standing and down trees to help reconstruct stand histories, (3) measurements of light quality and quantity in the forest interior, (4) measurements of rainfall distribution and interception in the forest, (5) describing the structural dynamics of the winter snowpack in relation to forest canopy structure and understory vegetation pattern, (6) construction of topographic contour maps of the eight reference stands, and (7) monitoring the fecundity and mortality of tree species populations at yearly intervals using tagged and mapped individuals.

The 1983 snow-free season had cooler May and September air temperatures than either 1981 or 1982, but its June, July and August temperatures were intermediate. Total summer precipitation was 471 mm, almost twice the long-term average; more than 80% of this four-month summer total fell between 19 June and 29 July, and May and early June were quite dry. About 15 cm of heavy wet snow fell on 23 May, causing considerable mechanical damage to trees. The small Snowshoe Hare population caused very little damage to its preferred plant food species in 1983; the Tent Caterpillar population virtually disappeared between 1982 and 1983 after causing much defoliation of its preferred food plants in 1981 and 1982.

The species evenness and diversity of both vascular plant and terrestrial bryoid (bryophyte + lichen)

communities increased significantly in several reference stands in 1983 cf. 1981-82. Forbs, shrubs and terrestrial bryoids had higher cover in most stands in 1983 cf. 1981.

The line-intercept method gave species cover estimates that agreed very closely with those obtained by standard ocular assessments in plots and microplots of reference stands.

After three years of monitoring the shoot/thallus cover dynamics of selected plant species the following general trends have emerged: (1) deciduous woody plants produce leaves relatively early and maintain a broad "plateau" of shoot cover until heavy frost occurs; (2) herbaceous perennials usually have narrower, more peaked periods of maximum shoot cover; and (3) evergreen dwarf shrubs tend to decrease in shoot cover in early summer, then increase to a maximum in autumn.

Feather mosses grew most rapidly in June, peat mosses in July, whereas other wetland mosses had bimodal peaks of height growth in early and late summer of 1983.

Two phenological spectra based on vegetative (leaf maturation) and reproductive (flowering) criteria were constructed, using vascular plant species found in the eight reference stands, based on data from 1982 and 1983. Each plant growth-form seems to have a typical pattern of phenological behavior. Comparisons of 1982 cf. 1983 phenology and phenological variations among stands were made.

Regression equations for estimation of shoot biomass and leaf area from shoot cover estimates are now available for 36 important forb species of the Southern Boreal Subzone. Simple linear equations give very acceptable estimates, with coefficients of determination (R^2) clustered around 0.85.

The age structures of living and standing dead tree populations are being documented using a combination of conventional and non-conventional techniques. This work and associated studies of (1) tree dispersion on stem maps of reference stands, and (2) dead and down trees and their decay processes are leading to improved models of plant succession and stand history for the Southern Boreal Subzone.

Computer-drawn topographic contour maps of the reference stands are now available, permitting correlation studies of vegetation and topography. It appears that microtopography plays an important role in limiting the recruitment of trees.

Measurements of rainfall distribution and light quality in the forest interiors of reference stands both lead to the conclusion that the forest canopy does indeed control the quantity and quality of resources available to understory members of boreal forest ecosystems.

Bird species richness during the snow-free season was generally higher in 1983 cf. 1982. In both years peak richness occurred in June. Maximum bird species richness

was found in the oldest and botanically richest stands.

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1. INTRODUCTION

1.1 BACKGROUND REVIEW

The purposes of this report are to summarize the accomplishments of the SEADYN project during 1983-84 and indicate new directions anticipated in 1984-85. As such it should be considered in conjunction with two earlier reports (La Roi and Ostafichuk 1982 = "First Report"; La Roi, Ross, and Ostafichuk 1983 = "Second Report") in which 17 major objectives initiated during 1981 and 1982 are described, along with some preliminary results from the research activities of those two years. A more comprehensive summary of SEADYN findings is planned after the fifth (1985) field season has been completed (i.e. at the end of the first five-year phase of the project).

The SEADYN project was conceived to fulfill a need for more detailed information on and a better understanding of boreal forest structure and function. A permanent plot design was chosen, not only because it allows for the repeated observations necessary to trace intraseasonal, seasonal, and annual changes, but also because it permits and fosters the integration of information on different components of the same ecosystem. During the 1983 field season, observations of intraseasonal changes in biological and physical ecosystem components were continued for the third year (First Report - Objectives 4, 5, 6, 7, 8, 12, 13, 14; Second Report - Objective 17). In addition, detailed

observations on the physical structure and spatial arrangement of the forest canopy and understory begun in 1981 (First Report - Objectives 4, 5, 10, 11) were taken to a finer level of resolution. The interlocking and cumulative design of the SEADYN studies should provide a solid foundation for conclusions about boreal forest dynamics at the end of the first phase of the project in 1985.

1.2 SEADYN PROJECT STUDIES CONTINUED IN 1983

All of the 17 major objectives outlined in the First and Second Reports were continued in 1983. Changes in methodology, if any, are specified in the Methods section below; otherwise it may be assumed that methods described in the First and Second Reports were also used in 1983.

1.3 SEADYN PROJECT STUDIES INITIATED IN 1983

The seven major objectives initiated in 1983 were:

(18) Develop a rapid and objective method for estimating the shoot/thallus cover of plants at short time intervals that minimizes observer impact and can be performed by relatively inexperienced personnel.

(19) Estimate the death dates of mapped down and standing dead trees in order to reconstruct stand history and study decay processes and colonization sequences by plants on these stems.

(20) Study the spectral dynamics of light in the forest interior .

(21) Compare the amount of summer precipitation that reaches the ground in the open and under the over- and understory canopies of the eight reference stands.

(22) Examine the physical structure and energy relationships of the winter snowpack in relation to forest canopy structure and micro-scale vegetation patterns.

(23) Draw topographic contour maps of the eight reference stands and selected 5 x 5 m plots within them in order to correlate meso- and microtopography with plant species composition, tree growth, seedling recruitment, snowpack properties, etc.

(24) Monitor the mortality and fecundity of tree species populations at yearly intervals using tagged and mapped individuals.

2. METHODS

2.1 REVIEW

Unless otherwise stated below, methods and procedures described in the First and Second Reports were used in essentially unmodified form in 1983.

2.2 VASCULAR PLANT SHOOT COVER, LEAF AREA, AND ABOVE-GROUND BIOMASS RELATIONSHIPS

Laboratory analysis of the shoots collected in 1981 and 1982 was completed during 1983 by the methods specified in the First and Second Reports. Regression models using shoot cover to estimate shoot biomass or leaf area for herbaceous species and low shrubs were derived and are discussed in Results section 3.6.

In order to determine whether equations developed from specimens collected in 1981 and 1982 were valid for plants of the same species in another year, 10 individuals of 15 major herbaceous forb species were collected from a range of sites in late June 1983. Field and lab procedures were the same as those detailed for the 1981-82 specimens used to generate the equations.

Statistical analyses of the 1981-82 data set for medium and tall shrubs showed that shoot cover is not a good predictor of biomass or leaf area of these growth-forms. Other studies have shown that basal stem diameter is an excellent predictor of total biomass for certain shrub species (Martin et al. 1981, Smith and

Brand 1983). Therefore, 10-30 ramets of 11 major medium and tall shrub species were collected in mid-July 1983 from the range of sites occupied by each species. A stratified random sampling system was used to ensure that an adequate range of sizes was sampled. Basal diameter and height of each stem were measured in the field, but shoot cover was not estimated. Leaves were separated from the stem and pressed for leaf area determination in the laboratory, and dry weights of stem and leaf tissues were subsequently determined separately.

2.3 PHENOLOGICAL OBSERVATIONS OF VASCULAR PLANTS

The method used for phenological observations of vascular plants in 1983 was essentially the same as in 1982; that is, wherever possible observations were made on populations rather than on isolated individuals, and the proportion of the population in each phenophase was estimated. However, in some cases where species occurred only as isolated individuals rather than in distinct groups, it was necessary to monitor the development of single stems. It should be noted that the distinction between "population" and "individual" in clonal species, in which category most resident species fall, is a hazy one, and one not easily made in the field. Thus, "population" in the current context implies only a distinct group of stems of a single species, without regard to origin.

An effort was made to reduce the time spent on phenological observations in 1983. Species were observed only in stands in which they were common, with the proviso that each species be monitored in at least one of the eight reference stands. The number of populations per species observed in each stand was reduced from three to two. However, the frequency of observations was increased from weekly intervals throughout the 1982 field season (May-August) to every five days from 1 May to 15 June 1983, and weekly thereafter through the first week of October.

Slight modifications were made in the phenophase classification system used in 1982. The purposes of these changes were to remove several ambiguities and to make the categories of one growth-form as parallel as possible to those for another. The classification system used in 1983 appears in Table 1.

2.4 POPULATION STRUCTURE OF TREE SPECIES

Because trees presumably utilize or immobilize a major share of available resources in closed boreal forests, the dynamics of survival, growth and reproduction of other members of the biotic community, or of the microclimate impinging upon them, must be interpreted with reference to their positions relative to the forest canopy. Of course, the tree populations themselves undergo structural changes over time. We intend to study these changes by a combination of (a)

Table 1. Classification system for field observations of vegetative and reproductive phenology in 1983.

1. Vegetative Shoot (bud, stem, leaves)

A. Herbaceous Forbs and Graminoids

0 - plant dormant; no above-ground live
2 - shoot or leaves emerging from soil; leaves v small and rolled or folded
3 - all leaves immature
4 - mature leaves present
5 - shoot has ceased vegetative growth; all leaves mature
6 - senescing leaves present
7 - shoot dead

B. Evergreen and Wintergreen Forbs and Graminoids

0 - shoot dormant but some of previous year's leaves green
2 - very small new leaves visible
3 - all new leaves immature
4 - mature new leaves present
5 - shoot has ceased vegetative growth; only mature leaves present
8 - old leaves green
9 - old leaves senescing

C. Needle-leaf Trees

0 - buds dormant; evergreen foliage mature
1 - buds swollen but scales cover leaves
2 - needles emerging; green visible; pine shoots in 'candle' stage
4 - needles fully elongated but soft and light green
5 - needles mature and of normal color
6 - larch needles yellowing and/or falling
7 - larch needles shed
8 - old leaves green
9 - old leaves senescing

D. Broad-leaf Deciduous Shrubs and Trees

0 - buds dormant; old leaves shed and decomposing or a few attached/crisped
1 - buds swollen but scales cover leaves
2 - green leaves visible but v small and often folded or rolled
3 - leaves partly expanded
4 - leaves fully expanded but soft and light green
5 - leaves mature and of normal color and texture
6 - senescing leaves present
7 - leaves shed or dead
8 - no dormant terminal buds present
9 - dormant terminal buds formed

continued ...

Table 1. Concluded

E. Broad-leaf Evergreen Shrubs

0 - buds dormant; evergreen foliage mature
1 - buds swollen but scales cover leaves
2 - green leaves visible but v small and often folded or rolled
3 - leaves partly expanded
4 - leaves fully elongated but soft and light green
5 - leaves mature and of normal color and texture
8 - old leaves green
9 - old leaves senescing

2. Reproductive Structures

A. Angiosperms with "showy", Perfect Flowers

0 - no floral buds visible
1 - floral buds visible but dormant
2 - floral buds swelling
3 - flowers open
4 - immature fruit visible
5 - ripe fruit present
6 - fruits dehiscing, seeds dispersing

B. Plants with Unisexual Flowers, Cones, Sori, Strobili

0 - no floral buds visible
1 - reproductive structures visible but dormant
3 - reproductive structures open - pollen, spores shed when agitated
4 - immature fruit present (cones, pistillate catkins)
5 - ripe fruit present
6 - shedding seeds

comparing the structure of tree populations in stands of different age on the same habitat type, (b) examining contemporary changes in tree populations by measuring growth rates and monitoring births and deaths in the existing populations, and (c) reconstructing the development of current stands by analyzing increment cores of live trees, and identifying and estimating the death dates of standing dead and down trees.

2.4.1 LIVE TREES

An important objective for the 1983 field season was to more completely measure the physiognomy and stature of the forest canopies of the eight reference stands, as well as the population age structures of the tree species which compose them. This work built on stem mapping information collected in 1981 and 1982, which consisted of diameter breast height (DBH) and location coordinates for each living stem >2.5 cm DBH in the 50x50 m stands (First Report, section 3.6). It was not possible to measure every mapped stem in all reference stands during 1983, so crown characteristics were measured on all stems >2.5 cm DBH within the following sectors: stand nos. 1, 2, 3, 7 - entire 50x50 m; stand nos. 4, 5, 6 - central 40x40 m; stand no. 8 - central 30x30 m. Tree parameters measured were: total tree height and live crown depth (Suunto clinometer); crown width (both N-S and E-W orientations); crown opacity or "filling factor" (i.e. % "filled" when viewed from

below); and direction and degree of stem lean.

Age and diameter growth rates were also obtained for subsets of the mapped trees in the reference stands. Increment cores were taken at 25 cm above ground level for all trees >7.5 cm DBH within the following sectors: stand nos. 1, 2, 3, 7 - central 40x40 m; stand nos. 4, 5, 6 - central 30x30 m; stand no. 8 - central 20x20 m. Trees 2.5-7.5 cm DBH were cored throughout the eight 50x50 m stands according to the following sampling scheme: stand nos. 1, 2, 3 - all stems in size range; stand nos. 5, 7, 8 - one randomly selected 2.5-7.5 cm stem per 5x5 m plot; stand nos. 4, 6 - all *Picea glauca* stems in size range, one randomly selected *Abies balsamea* per 5x5 m plot.

Ages were estimated from ring counts on mounted and sanded cores under a dissecting microscope. Corrections for age at core height were: *Populus tremuloides*, +2 years; *Betula papyrifera*, *Pinus banksiana*, +5 years; *Abies balsamea*, *Picea glauca*, *P. mariana*, +7 years. Radial growth increment was measured to the nearest 0.1 mm in 10-year units starting in 1982 and working backwards to the center of the tree. Annual ring widths were measured for selected cores from each stand.

Stems of immature trees <2.5 cm DBH of all species were mapped and tagged in May and June 1983. All individuals within centrally located 5x5 m plots were

included; the number of plots censused in each stand was inversely related to density of seedlings, with the condition that at least five plots be sampled. The number of plots censused in the eight stands were: stand nos. 4, 7 - 5 plots; stand nos. 6, 8 - 10 plots; stand nos. 1, 3 - 50 plots; stand nos. 2, 5 - 100 plots. Basal diameter, height, and location coordinates were recorded for each stem, as well as observations on local substrate and browsing damage. For *Picea mariana*, which reproduces by layering as well as by seed, only the oldest stem in a group of layered individuals was tagged and measured. Stems of *Abies balsamea*, *Picea glauca*, *P. mariana*, *Populus tremuloides*, and *Larix laricina* were aged by counting terminal bud scars; a sample of stems of these species harvested outside the stands gave reasonable agreement between ages determined in this way compared with ring counts from cross-sections at the root collar. Bud scar counts seriously underestimate stem age for *Pinus banksiana* and *Betula papyrifera*, the former because of frequent browsing by hares, and the latter because of the indistinctness of the scars. Therefore, age was estimated for these species by collecting matching stems of similar diameter outside the plots and aging them by ring counts on cross-sections.

2.4.2 CURRENT POPULATION PROCESSES

The mapped and tagged stems of all sizes provide a framework for tracking population dynamics of tree

species in future years. Mortality, growth, and fecundity rates can be monitored and grouped into age- or size-specific averages. This effort was begun in 1983 by recording mortality among stems >2.5 cm DBH that had been alive when mapped in 1981 or 1982.

Ocular estimates of the 1983 *Picea glauca* cone crop were made in late July on all cone-producing trees in the reference stands.

2.4.3 DEAD AND DOWN TREES

Several types of evidence were used in an attempt to determine the death dates of identifiable logs and snags. They were:

1. The minimum time since a tree has fallen can be determined from the maximum age of woody species which have become established on the log.

2. The time elapsed since a tree has fallen can be determined very accurately by the ring pattern of trees bent by its fall. The down-side of the tree bent towards the log will have compressed rings beginning suddenly in the year of fall, and the up-side away from the fallen tree will have expanded, discolored rings beginning in the fall year.

3. Previously suppressed trees often show a dramatic growth response (increase in radial increment) soon after the death and/or fall of a large neighbor.

4. If a reasonably solid section of wood can be extracted from somewhere along the trunk of a down or

standing dead tree, it may be possible to cross-date it with a ring-width chronology developed from live trees in the stand, and hence determine the year the outermost growth ring was formed.

5. A down tree lying under a tree dateable by any of the previous methods fell on the same or some earlier date.

If the time interval since tree fall is well correlated with a decay classification developed for the local species and sites, a rough estimate of the earliest possible fall date may be made on the basis of the state of decay of a log.

Beginning in August 1983, maps of all recognizable down trees >5 cm DBH were made within central sectors of each reference stand. Sector size was based on the number of down stems in the stand, and ranged from 30x30 m to the entire 50x50 m stand. The maps include the location of the stump of each tree and the orientation of different pieces of shattered trunks. Where one log crossed another, the map indicates which stem was on top. For each tree, species, diameter, and decay class (Table 2) were recorded. Where the species was not obvious, a small wood sample was taken for laboratory identification. Where the wood was not too decomposed, a section was taken for dating by Method 4 above. Any other evidence in the stand which would help date the log directly or indirectly by Methods 1, 2, 3, 5

Table 2. Wood decay classes[a] for dead trees in reference stands of the Hondo - Lesser Slave Lake study area.

Decay Class and Subclass	Definition
1	Tree whole and undecayed; bark, branches and twigs present; colonization by epiphytes only (lichens and bryophytes).
1A	Tree very sound but bark and twigs mostly lacking (standing dead trees often in this subclass).
1B	Tree very sound but small patches of bark missing.
2	Tree reasonably sound but wood is soft and rotting in places; some bark and branches still present; colonization still mainly by epiphytic lichens and bryophytes.
3	Wood with fungi present throughout yet some of it remains hard, fibrous, etc.; colonization by bryophytes beginning, especially near the ground surface.
3A	Wood mostly soft and weak.
4	Wood rotten, but still recognizable as wood; >50% of original wood fibers still recognizable; log is now partially to mostly moss-covered, and collapsing.
5	Wood mostly well decayed and humification advanced; log completely moss-covered and colonized by various vascular plants (herbs, shrubs, trees).
5A	About 50% of original woody biomass still present as organic material.
5B	Less than 50% of original woody biomass remaining.
5C	Humification nearly 100%; log residue scarcely recognizable except for linear dispersion of its former colonizers.

continued ...

Table 2. Concluded

Decay Class and Subclass	Definition
Additional subclasses which can apply to any of the 5 major decay classes.	
D	More decomposition at base of tree or butt end of log.
E	More decomposition at top of tree.
F	Outer bark completely gone.
Notation on tree condition when it fell to the ground:	
I	Trunk broke off above tree base, leaving erect stump.
II	Trunk broke off at tree base, leaving roots in ground.
III	Tree uprooted; trunk not broken off.

[a] Classification designed and applied by Myron Smith.

above were investigated by the appropriate means. At the same time, an effort was made to date down trees of the major species just outside the reference stands by the methods detailed above. Diameter and decay class were recorded, and a relationship was sought between these two measures and the time elapsed since fall date for the relevant species in each stand.

Several of the more dependable methods discussed above estimate tree fall date, not tree death date. In order to study the sequence and duration of events between tree death and tree fall dates, standing dead trees outside the plots were examined. Species, diameter, state of decay, decay-producing organisms, and proportion of original stem remaining were noted. Trees were then felled and a wedge removed for cross-dating.

2.5 ALTERNATIVE METHOD OF ESTIMATING SHOOT COVER

There is no question that ocular estimation of plant cover in quadrats, particularly those as large as 5x5 m, is subject to some systematic error arising from observer bias. However, in situations such as the first phase of the SEADYN project, where the primary objective is to monitor relative changes over time, and where the observers are the same from sampling date to sampling date, the method has proven successful in documenting intraseasonal patterns which recur year after year (section 3.3). Nevertheless, in anticipation of a time when project objectives might shift, or when observers

might change at more frequent intervals, it was decided to test and calibrate a line-intercept method for estimating cover of shrubs, herbs, bryophytes, and lichens.

In May 1983 10 pairs of adjacent corner posts were chosen randomly around the perimeter of each reference stand. A 5 m tape was stretched between two pins placed 30 cm from the posts towards the interior of the stand. Kneeling outside the plot, the observers recorded for each species the centimeters of live plant tissue intercepted by a vertical projection of one edge of the tape. Bryophyte and lichen interception was measured under a 3 m segment of the tape, while vascular plants were measured along the entire 5 m length. Centimeters of overlap between different shoots of the same vascular species were also estimated. The locations chosen in May were resampled three more times in 1983, concurrently with the June, July, and August monthly surveys of vascular species cover in 5x5 m plots.

2.6 SPECTRAL DYNAMICS OF LIGHT IN THE FOREST INTERIOR

A common attribute of all forest plant communities is their hierarchical stratification in relation to the source of radiant energy. Species are normally grouped in horizontal layers or "strata". Each stratum differentially absorbs and reflects incident radiant energy of different wavelengths, thereby reducing

the quantity and altering the quality of light available to the strata below it. The location of these strata, their cover, and the kinds of species that occupy them vary over time, as well as with site characteristics. In order to investigate light quantity and quality as potential mechanisms for over- and understory interactions in the eight SEADYN reference stands, a study of the spectral dynamics of light in their forest interiors was initiated in 1983.

The light measurements in 1983 were made in preparation for a comprehensive study in 1984. Thus the immediate goals were: (1) to estimate the temporal and spatial variation in light spectra within a stand in order to develop an appropriate sampling design; and (2) to become familiar with the features and limitations of the available equipment. The quantity of incoming energy in different light wavelengths (range 350-750 nm) was determined during the mid day period of four cloudless days in early August, 1983, using a LICOR LI-1800 spectral radiometer. 30-35 readings per day were taken at different points within four reference stands. Each day's readings were transferred to cassette tapes for storage and laboratory analysis.

2.7 RAINFALL INTERCEPTION DURING SUMMER STORMS

The forest canopy and subordinate vegetation layers also influence the amount of precipitation which reaches the forest floor. Although in some cases trees

can enhance the effective precipitation by trapping fog or dew (Geiger 1965), intercepted precipitation usually evaporates and constitutes a loss to the system. In fact, dry microsites on the forest floor (e.g., around *Picea* or *Abies* tree bases) may receive almost no direct rainfall, and this may explain much of the local patchiness of understory vegetation. Consequently, a study was begun in 1983 to assess the overall reduction in rainfall reaching the ground effected by various types of boreal forest canopies, and the within-stand variability in this characteristic. Plastic cups (8 cm lip diameter) were placed at each corner of the 100 5x5 m plots of one reference stand prior to three storms in late July and August. Several cups were placed in an open area nearby. Once the rain had stopped and dripping from the canopy had ceased, the cups were retrieved and the volume of water in each was measured.

2.8 TOPOGRAPHY AND VEGETATION

In order to describe and interpret the topographic relations of plant growth-forms, species and community components in the eight reference stands, topographic contour maps were developed for each stand as well as for two 5x5 m plots in each stand. The smaller plots were chosen on the basis of vegetation structure and composition; one was considered typical of the stand as a whole, and the second was a common variant. The contour maps were based on elevations determined with a

Debenham levelling device (which consists of two rigid, clear plastic tubes mounted on graduated wooden staffs and connected by a 7 m length of water-filled clear Tygon tubing; the staffs are placed at two locations and the heights of their water menisci recorded and compared to determine their relative elevations). Elevations were measured at 5 m intervals in the 50x50 m stands and at 7.1 dm intervals in the 5x5 m plots.

Although it was anticipated that plant cover data from the monthly surveys (section 3.3, First Report) could be used to study the covariance of vegetation and topography in the reference stands as a whole, more detailed vegetation data were needed to investigate this relationship at the 5x5 m scale. The two mapped plots in each stand were gridded into 49 7.1x7.1 dm blocks. The presence of each vascular, bryophyte, and lichen species in each block was recorded, as well as the percent cover of several dominant understory species in each stand. Tree species were treated separately; the crowns of mature trees were projected on a map; and the location of each seedling was mapped. Also included in this map were the locations of rotting logs and other large woody debris.

2.9 PHYSICAL CHARACTERISTICS OF THE 1983-1984 SNOWPACK

The structural dynamics of the snowpacks in stand nos. 1, 3, 7, 8 and an old white spruce stand were

monitored during the winter of 1983-84. All measurements were made at 4-week intervals throughout the winter (December-March).

2.9.1 Api: Snow on the Ground

Snowpits were used to assess snow stratigraphy, providing information on the temporal development of the snowpack within each of the reference stands. During the summer of 1983, two rows of seven stakes each were driven into the ground. Each pair of stakes was the site for one snowpit at which the following data were recorded: temperature gradient; total snow depth; thickness, density, hardness, and grain size and shape, of each snow horizon. A modified Adams and Barr (1974) snow kit was used to determine these properties.

A snow course was set up in each of the five stands in order to monitor the within-site spatial variability of the snowpack. This course consisted of eight permanent sample points. From each point three vertical snow cores were taken with a Mount Rose snow corer. The means, variances and ranges of depth, density and water equivalency of the snowpack will be determined from the cores, in order to compare stands and dates.

2.9.2 Qali: Snow on Trees

Qali accumulation was measured by qalimeters, simple mechanical devices that simulate tree branches. The device is described in detail by Pruitt (1958).

Qualimeters have been established in each of the five aforementioned stands in order to monitor the between-stand variation in snow accumulation on trees. During the summer of 1984, several qalimeters will be established in each stand at different heights in order to determine vertical differences in qali accumulation.

2.10 OBLIQUE COLOR AIRPHOTOGRAPHY OF REFERENCE STANDS AND STUDY AREA

On 29 September 1983, oblique airphotos were taken of the eight reference stands and surrounding parts of the Hondo - Lesser Slave Lake study area by J. Fyles, G. La Roi, and M. Ostafichuk, from a Bell Jet Ranger helicopter supplied by the Research Management Division of Alberta Environment. Prior to taking the photos, plastic tarps of different colors were placed on the ground at the corners of the reference stands to aid in locating them and precisely locating features on the resulting pictures. Kodachrome 64 film was used. Photographs included: (1) general oblique pictures of the vegetation mosaic surrounding each reference stand; (2) near-vertical pictures of the four corners of each reference stand from *ca.* 50 and 150 m above ground; and (3) oblique pictures of the forest canopy from several compass orientations and elevations. Sky conditions were excellent, with <10% cloud and very light winds. All photos were taken between 1200 and 1400 hrs Mountain Daylight Time (MDT).

3. RESULTS AND DISCUSSION

3.1 METEOROLOGICAL MEASUREMENTS IN 1983

Table 3 lists daily maximum, minimum and mean air temperatures at the Hondo meteorological station, located in an open field behind the base camp, for the 1 May to 30 September 1983 period. Maximum and minimum temperatures at the NW Station, which is located in a small opening in a 20 year-old aspen stand about 30 km west of camp along Highway 2, were within 1°C of Hondo on most days, and are therefore not included in Table 3.

Mean daily temperatures at the Hondo and Northwest stations in 1983, as compared with those of the previous two summers and with the 30-year normals for Slave Lake (Environment Canada 1975), were:

	Slave Lake	Hondo			Northwest		
	(1941-1970)	1981	1982	1983	1981	1982	1983
May	9.1	10.8	9.5	7.0	10.4	8.9	6.6
Jun	13.1	9.5	14.4	11.6	10.3	14.5	11.2
Jul	15.7	13.9	15.5	14.2	14.5	15.2	14.1
Aug	14.1	14.7	10.8	13.4	15.1	11.2	13.4
Sep	9.2	7.7	8.2	5.2*	8.0	9.4	4.8
mean	12.2°C	11.3	11.7	10.3	11.7	11.8	10.0

* Substituted NW Station data for missing Hondo data 28, 29, 30 September.

Table 3. Daily air temperature data from the Hondo station of the SEADYN study area for the period 1 May to 27 September 1983. Data are from calibrated Lambrecht thermo-hygrographs mounted 1.5 m above ground in standard Stevenson screens; temperatures are °C.

HONDO STATION (55°4' N Lat 114°30' W Long)

Month / Day	Min	Max	Mean	Month / Day	Min	Max	Mean	Month / Day	Min	Max	Mean
May				June				July			
1	-9	11	1	1	-1	15	7	1	9	21	15
2	-5	4	0	2	-4	12	4	2	7	23	15
3	-7	12	2	3	-5	13	4	3	4	25	14
4	-4	15	6	4	1	17	9	4	10	20	15
5	-1	9	4	5	0	18	9	5	8	25	16
6	0	13	6	6	-1	20	10	6	7	22	14
7	4	14	9	7	-1	21	10	7	11	20	16
8	-2	10	4	8	-1	23	11	8	7	16	12
9	1	10	6	9	4	23	14	9	5	21	13
10	-8	13	2	10	4	23	14	10	5	22	14
11	-6	17	6	11	-2	17	8	11	4	20	12
12	-4	17	6	12	-1	15	7	12	3	19	11
13	-1	8	4	13	1	23	12	13	3	21	12
14	-11	10	0	14	3	25	14	14	8	15	12
15	1	14	8	15	9	27	18	15	8	12	10
16	3	15	9	16	12	26	19	16	7	15	11
17	-1	17	8	17	10	27	18	17	5	18	12
18	-1	17	8	18	10	14	12	18	5	22	14
19	2	17	10	19	8	16	12	19	8	26	17
20	2	14	8	20	8	19	14	20	13	22	18
21	2	17	10	21	5	16	10	21	9	14	12
22	2	11	6	22	-2	14	6	22	9	24	16
23	-6	4	-1	23	6	20	13	23	12	28	20
24	-6	23	8	24	10	18	14	24	12	25	18
25	1	22	12	25	3	11	7	25	12	24	18
26	-1	17	8	26	3	19	11	26	8	16	12
27	-3	22	10	27	4	20	12	27	7	13	10
28	-1	28	14	28	7	24	16	28	9	22	16
29	4	30	17	29	6	26	16	29	5	22	14
30	4	25	14	30	11	23	17	30	5	24	14
31	1	23	12					31	7	27	17
$\bar{X}$	-1.6	15.5	7.0	$\bar{X}$	3.6	19.5	11.6	$\bar{X}$	7.5	20.8	14.2

continued ...

Table 3. Concluded

HONDO STATION (Concluded)

Month / Day	Min	Max	Mean	Month / Day	Min	Max	Mean
August				September			
1	9	26	18	1	10	18	14
2	8	27	18	2	6	19	12
3	4	21	12	3	3	18	10
4	1	21	11	4	4	15	10
5	5	26	16	5	-5	8	2
6	10	22	16	6	-2	13	6
7	3	21	12	7	-1	11	5
8	3	24	14	8	3	11	7
9	4	26	15	9	-4	9	2
10	6	30	18	10	-5	12	4
11	14	20	17	11	-5	13	4
12	3	19	11	12	1	14	8
13	4	-	-	13	-	-	-
14	-	-	-	14	-	-	-
15	-	-	-	15	-1	11	5
16	1	19	10	16	0	7	4
17	5	17	11	17	-2	6	2
18	0	18	9	18	-2	1	0
19	0	19	10	19	-8	10	1
20	4	17	10	20	2	12	7
21	1	20	10	21	5	14	10
22	1	24	12	22	1	22	12
23	1	26	14	23	0	19	10
24	5	24	14	24	5	17	11
25	1	24	12	25	2	21	12
26	2	24	13	26	-5	18	6
27	1	24	12	27	-9	3	-3
28	1	21	11	28	-12	-	-
29	1	24	12	29	-	-	-
30	11	24	18	30	-	-	-
31	11	26	18				
$\bar{X}$	4.1	22.6	13.4	$\bar{X}$	-0.7	12.9	6.4

For the third consecutive summer, both Hondo and NW stations recorded lower-than-normal temperatures in 1983. Temperatures approached the 30-year average in August, but during the May-July period, which certainly exerts the most influence on current-year growth and phenology, temperatures were 1.5 degrees or more cooler than normal. In comparison to 1981 and 1982, May and September 1983 temperatures were the coolest of the three years, while those of June, July, and August were intermediate.

Table 4 lists daily precipitation amounts received at the Hondo meteorological station between 1 May and 31 August 1983. These figures indicate that more than 80% of the precipitation during the 4-month summer period occurred between 19 June and 29 July. During that 41-day interval only 11 days passed without measurable precipitation, and on 8 days more than 25 mm of rain fell. The most violent of these storms, which began on the evening of 20 July and continued through the next day, deposited 84 mm on Hondo but decreased in intensity toward the west. Because of the patchy nature of the rainfall pattern for this and other storms, the Hondo station received 40 mm more rain than rainfall collectors located outside the two nearest reference stands during July, and about 90 mm more than the most distant stands, i.e. nos. 5 and 6. During the other three months, precipitation at Hondo was about average for the study area as a whole. Over the May-August period, total

Table 4. Daily precipitation data from the Hondo Station of the SEADYN study area for the period 7 May to 30 September 1983. Data are from a 15 cm diameter receiver mounted 0.5 m above ground, measured in mm each morning at 0700 hrs MDT.

Day	May	June	July	August	September
1	- [a]	4.0	6.2	-	-
2	T [b]	0.6	1.5	-	11.0
3	0.6	-	-	1.6	1.0
4	1.0	-	3.5	3.8	-
5	1.0	-	34.0	-	5.4
6	212	-	7.4	0.3	-
7	210	2.0	2.7	-	0.6
8	0.1	-	4.4	-	0.2
9	1.5	-	32.1	-	-
10	-	4.2	-	-	9.2
11	-	12.8	-	-	-
12	-	-	-	0.6	-
13	0.3	0.3	2.6	-	-
14	-	-	19.5	12.2	0.8
15	-	-	5.1	2.5	3.0
16	-	0.2	5.8	0.4	1.0
17	0.2	-	8.1	2.6	6.8
18	-	-	4.5	0.1	0.3
19	-	37.7	4.9	-	-
20	0.1	1.8	-	3.4	-
21	3.6	15.5	50.0	-	-
22	1.4	2.6	34.2	-	-
23	8.6	0.3	-	-	-
24	5.0	-	-	0.4	-
25	-	27.6	1.6	-	-
26	-	24.9	27.8	-	2.2
27	1.7	-	14.0	-	-
28	-	-	2.2	0.1	-
29	-	3.2	1.9	-	-
30	-	-	-	1.0	-
31	1.0		-	-	
Σ	30.3	137.7	274.0	29.0	41.5

[a] - = no precipitation.

[b] T = trace only; often caused by dew or melted frost.

precipitation at Hondo was 471 mm, while precipitation at the other eight rain gauges ranged from 388 to 435 mm.

As the table below shows, total precipitation during the summer of 1983 was almost twice normal. For much of July and August, water was ponded in areas normally dry, and insects and mushrooms of all sorts were plentiful. Nevertheless, May and early June were quite dry, which may have had some impact on biological processes (e.g., seed production).

	Slave Lake (1941-1970)	Hondo 1981	1982	1983
May	45.2	9.1	15.4	30.3
June	67.8	74.9	11.9	137.7
July	79.5	120.3	130.2	274.0
August	65.5	9.8	97.7	29.0
4-mo total	258.0 mm	214.1	255.2	471.0

Another noteworthy meteorological event during May was a brief, heavy snowstorm which began early on the morning of 23 May and continued until noon, depositing as much as 15 cm of wet snow in places. Although the snow had melted by the following day, several trees in the reference stands were toppled.

3.2 MONTHLY SURVEY OF PLANT COMMUNITIES DURING THE SNOW-FREE SEASON

Six monthly surveys of vascular shoot and bryoid thallus cover in quadrats were conducted between May and October 1983 (see First Report, Methods section 3.3). A snowfall during the first week of November precluded a

cover survey during that month.

3.2.1 August 1983 Synthesis Table

Table 5 shows the mean cover estimates for vascular, terrestrial bryophyte, and terrestrial lichen species in 25 5x5 m plots in each reference stand in August 1983. Species are arranged in order of their ecological association with the three habitat types, beginning with those restricted to well drained aeolian sands and ending with those restricted to poorly drained peatlands. The format is identical to that of the August 1981 and August 1982 synthesis tables in the First and Second Reports, with the exception of the following nomenclatural changes based on the 1983 revision of Flora of Alberta (Packer 1983):

old name		new name
Rubus acaulis	=	*Rubus arcticus*
Rubus strigosus	=	*Rubus idaeus*
Lonicera villosa	=	*Lonicera caerulea*
Solidago decumbens	=	*Solidago spathulata*
Hieracium canadense	=	*Hieracium umbellatum*
Pyrola secunda	=	*Orthilia secunda*
Pyrola virens	=	*Pyrola chlorantha*
Aster juncIformis	=	*Aster borealis*
Dryopteris spinulosum	=	*Dryopteris carthusiana*
Carex foenea	=	*Carex siccata*

Also, several identification problems have been resolved:

previously		now
Carex umbellata	=	*Carex richardsonii*
Carex rostrata	=	*Carex aquatilis*
Carex aurea	=	*Carex concinna*
Carex canescens	=	*Carex vaginata*
Lycopodium tristachyum	=	*Lycopodium complanatum*

Table 5. Synthesis table showing the estimated % cover of major plant growth-forms[a] and species in the eight reference stands of the Hondo - Lesser Slave Lake area in north central Alberta (August 1983).

GROWTH-FORM / *Species*	Reference Stand Number							
	Aeolian Sand H.T.				Glacial Till H.T.		Peatland H.T.	
	1	2	3	4	5	6	7	8
TREE	*7.46*	*7.98*	*16.86*	*41.42*	*32.24*	*35.04*	*17.92*	*25.48*
Pinus banksiana	7.38	7.88	13.14	.420	.	.	.	.
Populus tremuloides	.080	.020	.764	1.96	17.24	9.76	.	.
Picea glauca	.004	.080	2.38	23.68	14.80	17.08	.	.
Betula papyrifera	.	.	.228	.523	.124	.640	.	.
Abies balsamea	.	.	.120	13.72	.	7.36	.	.
Populus balsamifera	.	.	.	.	.080	.200	.	.
Picea mariana	.	.	.225	1.12	.	.	17.20	25.32
Larix laricina	.	.	.	.	.	.	.724	.161
SHRUB	*26.01*	*29.58*	*26.85*	*1.64*	*19.54*	*17.47*	*14.52*	*8.13*
Arctostaphylos uva-ursi	14.68	11.62	.824	.	.	.	.	.
Amelanchier alnifolia	1.09	.072	.040	.	.084	.205	.	.
Shepherdia canadensis	.201	.904	.	.	.	.	.	.
Prunus pensylvanica	.112	.296	.880	.	.	.360	.	.
Prunus virginiana	.	.	.	.	.	.	.	.
Linnaea borealis	.744	.772	5.12	1.01	8.6	4.14	.004	.341
Rosa woodsii	.	.080	.	.	.	.	.	.
Rosa acicularis	.877	2.42	2.06	.030	1.63	1.73	.	.328
Vaccinium myrtilloides	.900	1.08	1.74	.051	.	.	.	.045
Vaccinium vitis-idaea	6.02	5.62	2.10	.004	.044	.024	.180	.797
Alnus crispa	1.24	5.84	11.68	.	.	.	.	.

continued ...

Table 5. Continued

GROWTH-FORM	Reference Stand Number							
Species	Aeolian Sand H.T.				Glacial Till H.T.		Peatland H.T.	
	1	2	3	4	5	6	7	8
Rubus idaeus	.100	.184	1.65	.	.040	.244	.	.
Salix bebbiana	.040	.040	.	.	.	.	.	.080
Lonicera dioica	.	.	.040	.013	.317	.146	.	.
Viburnum edule	.	.	.	.498	3.68	3.46	.	.
Lonicera involucrata	.	.	.	.	1.45	4.56	.	.540
Ledum groenlandicum	.	.	.340	.0008	.	.020	5.26	5.56
Ribes triste	.	.	.	.0004	.380	.313	.	.
Rubus pubescens	.	.	.372	.029	3.72	2.08	.	.
Ribes glandulosum	.	.	.	.	.	.	.	.
Vaccinium caespitosum	.	.	.	.0012	.	.	.	.
Ribes lacustre	.	.	.	.	.018	.102	.	.0004
Symphoricarpos albus	.	.004	.	.	.020	.080	.	.
Betula pumila	.	.	.	.	.	.	3.54	.
Salix myrtillifolia	.	.	.	.	.	.	1.69	.301
Salix candida	.	.	.	.	.	.	.800	.
Salix pedicellaris	.	.	.	.	.	.	.976	.
Salix glauca	.	.	.	.	.	.	.	.
Salix arbusculoides	.	.	.	.	.	.	.060	.
Oxycoccus microcarpus	.	.	.	.	.	.	.712	.007
Andromeda polifolia	.	.	.	.	.	.	1.26	.
Lonicera caerulea	.	.	.	.	.	.	.040	.084
Cornus stolonifera	.	.	.	.	.	.	.	.
Salix pseudomonticola	.	.	.	.	.	.	.	.044

continued ...

Table 5. Continued

GROWTH-FORM	Reference Stand Number							
Species	Aeolian Sand H.T.				Glacial Till H.T.		Peatland H.T.	
	1	2	3	4	5	6	7	8
FORB	*3.21*	*5.22*	*15.13*	*2.00*	*31.64*	*20.75*	*5.42*	*1.98*
Antennaria racemosa	.040	.	.	.	.	.	.	.
Artemisia campestris	.001	.	.	.	.	.	.	.
Solidago spathulata	.059	.301	.	.	.	.	.	.
Erigeron glabellus	.073	.221	.	.	.	.	.	.
Aster laevis	1.02	1.31	.	.	.	.	.	.
Viola adunca	0.43	.038	.	.	.	.	.	.
Lilium philadelphicum	.	.	.008	.	.	.	.	.
Anemone patens	.094	.087	.020	.	.	.	.	.
Anemone multifida	.096	.096	.0008	.	.	.	.	.
Hieracium umbellatum	.031	.021	.012	.004	.	.010	.	.
Maianthemum canadense	1.31	1.52	2.68	.116	.602	.354	.	.
Galium boreale	.282	.146	.068	.012	.257	.306	.	.006
Geocaulon lividum	.100	.154	.005	.0004	.	.	.005	.005
Fragaria virginiana	.009	.	.060	.004	.221	.154	.	.
Pyrola chlorantha	.008	.	.016	.024	.	.012	.	.
Orthilia secunda	.008	.012	.328	.028	.015	.008	.018	.
Campanula rotundifolia	.025	.022	.005	.	.	.	.038	.006
Achillea millefolium	.001	.	.	.	.048	.042	.0004	.
Epilobium angustifolium	.0004	.	.364	.	.608	.324	.	.004
Aralia nudicaulis	.	.960	10.08	.561	6.48	5.68	.	.
Melampyrum lineare	.	.333	.	.	.	.	.	.
Viola renifolia	.	.	.216	.067	.576	.412	.	.
Actaea rubra	.	.	.	.0004	.141	.293	.	.
Cornus canadensis	.	.	1.26	.968	4.52	3.59	.	.124
Trientalis borealis	.	.	.0008	.075	.053	.062	.	.
Goodyera repens	.	.	.	.099	.005	.005	.	.
Petasites palmatus	.	.	.	.010	1.23	1.41	.	.589

continued ...

Table 5. Continued

GROWTH-FORM	Reference Stand Number							
Species	Aeolian Sand H.T.				Glacial Till H.T.		Peatland H.T.	
	1	2	3	4	5	6	7	8
Mitella nuda	.	.	.	.016	3.36	2.52	.104	.029
Mertensia paniculata	.	.	.	.020	3.24	3.39	.	.
Aster ciliolatus	.	.	.	.004	2.04	1.36	.	.0012
Aster conspicuus	.	.	.	.	.416	.220	.	.
Pyrola asarifolia	.	.	.	.	.206	.160	.	.
Galium triflorum	.	.	.	.	.025	.086	.	.
Lathyrus ochroleucus	.004	.	.	.	.125	.149	.	.
Fragaria vesca	.	.	.	.	.020	.118	.	.
Disporum trachycarpum	.	.	.	.	.	.040	.	.
Aquilegia brevistyla	.	.	.	.	.	.020	.	.
Vicia americana	.	.	.	.	.0004	.012	.	.
Smilacina trifolia	.	.	.	.	.	.	2.24	.
Menyanthes trifoliata	.	.	.	.	.	.	2.68	.
Potentilla palustris	.	.	.	.	.	.	.188	.
Orchis rotundifolia	.	.	.	.	.	.	.036	.004
Drosera rotundifolia	.	.	.	.	.	.	.022	.0008
Rubus arcticus	.	.	.	.	.	.	.004	.0008
Spiranthes romanzoffiana	.	.	.	.	.	.	.047	.189
Parnassia palustris	.	.	.	.	.	.	.006	.
Galium labradoricum	.	.	.	.	.	.	.022	.
Tofieldia glutinosa	.	.	.	.	.	.	.005	.
Aster borealis	.	.	.	.	.	.	.005	.
Corallorhiza trifida	.	.	.	.	.	.	.	.
Habenaria hyperborea	.	.	.	.	.	.	.001	.
Petasites sagittatus	.	.	.	.	.	.	.	.
Epilobium palustre	.	.	.	.	.	.	.0004	.

continued ...

Table 5. Continued

GROWTH-FORM / *Species*	Reference Stand Number							
	Aeolian Sand H.T.				Glacial Till H.T.		Peatland H.T.	
	1	2	3	4	5	6	7	8
Gentianella amarella	.	.	.	.	.	.	.	.
Rubus chamaemorus	.	.	.	.	.	.	.	1.02
Osmorhiza chilensis	.	.	.	.	.004	.	.	.
Moneses uniflora	.	.	.	.	.	.	.	.
Arenaria lateriflora	.	.	.	.	.	.	.	.
Taraxacum officinale	.	.	.	.	.	.	.	.
GRAMINOID	*1.56*	*.546*	*.590*	*.009*	*.279*	*.609*	*9.71*	*.900*
Carex richardsonii	.640	.194	.	.	.	.	.	.
Carex siccata	.0008	.016	.0004	.	.	.	.	.
Oryzopsis pungens	.501	.155	.0008	.	.	.	.	.
Oryzopsis asperifolia	.078	.031	.0004	.	.	.	.	.
Elymus glaucus	.007	.020	.	.	.	.005	.	.
Elymus innovatus	.318	.130	.560	.006	.004	.010	.	.024
Schizachne purpurascens	.020	.	.020	.	.	.009	.	.
Calamagrostis canadensis	.	.	.008	.002	.274	.532	.03]	.004
Agropyron trachycaulum	.	.	.	.	.	,004	.	.
Bromus ciliatus	.	.	.	.	.0008	.048	.	.
Calamagrostis inexpansa	.	.	.	.	.	.	.	.
Carex gynocrates	.	.	.	.	.	.	3.40	.401
Carex aquatilis	.	.	.	.	.	.	4.28	.004
Carex diandra	.	.	.	.	.	.	1.38	.
Carex interior	.	.	.	.	.	.	.208	.
Carex limosa	.	.	.	.	.	.	.0008	.
Triglochin maritima	.	.	.	.	.	.	.189	.
Carex concinna	.	.	.	.	.	.	.	.081

continued ...

Table 5. Continued

GROWTH-FORM / *Species*	Reference Stand Number							
	Aeolian Sand H.T.				Glacial Till H.T.		Peatland H.T.	
	1	2	3	4	5	6	7	8
Muhlenbergia glomerata	.	.	.	.	.	.	.	.
Carex vaginata	.	.	.	.	.	.	.	.386
Carex (yellow) sp.	.	.	.	.	.	.	.216	.
PTERIDOPHYTE	*.384*	*.025*	*.717*	*.011*	*.014*	*.030*	*.207*	*.166*
Equisetum variegatum	.064	.013	.0004	.	.	.	.	.
Lycopodium complanatum	.320	.008	.344	.	.	.	.	.
Equisetum arvense	.	.004	.	.007	.	.	.	.046
Lycopodium annotinum	.	.	.184	.	.	.004	.	.
Dryopteris carthusiana	.	.	.188	.	.	.	.	.
Lycopodium obscurum	.	.	.	.0008	.	.	.	.
Equisetum pratense	.	.	.	.003	.	.	.	.
Equisetum sylvaticum	.	.	.	.	.014	.026	.	.
Equisetum scirpoides	.	.	.	.	.	.	.089	.120
Equisetum fluviatile	.	.	.	.	.	.	.118	.
BRYOPHYTE	*6.92*	*13.14*	*65.93*	*62.20*	*4.82*	*47.93*	*59.58*	*76.39*
Polytrichum piliferum	.	.144	.	.	.	.	.	.
Ptilidium ciliare	.	.	.	.	.	.	.	.
Orthodicranum flagellare	.012	.	.320	.104	.	.016	.	.
Dicranum scoparium	.036	.020	.024	.	.	.	.	.
Polytrichum juniperinum	.160	.172	.040	.024	.	.	.044	.100

continued ...

Table 5. Continued

GROWTH-FORM	Reference Stand Number							
Species	Aeolian Sand H.T.				Glacial Till H.T.		Peatland H.T.	
	1	2	3	4	5	6	7	8
Ceratodon purpureus	.008	.012	.	.	.	.	.	.
Pleurozium schreberi	4.67	11.29	45.40	15.70	1.81	14.02	.820	39.80
Hylocomium splendens	1.35	.584	7.96	32.80	.752	15.48	1.94	34.40
Ptilium crista-castrensis	.012	.624	11.38	12.50	.308	8.40	.052	.100
Dicranum polysetum	.148	.228	.408	.156	.	.040	.	.480
Ptilidium pulcherrimum	.004	.036	.184	.356	.084	.100	.024	.144
Hepatic sp.	.	.	.	.	.	.	.	.
Brachythecium salebrosum	.	.024	.164	.204	3.16	4.72	.	.
Eurhynchium pulchellum	.	.	.004	.224	.960	1.33	.	.
Plagiomnium cuspidatum	.	.	.	.108	1.08	3.52	.	.004
Pylaisiella polyantha	.	.	.	.008	.124	.024	.	.
Rhytidiadelphus triquetris	.	.	.	.	.020	.	.	.
Drepanocladus uncinatus	.	.	.	.	.003	.200	.	.
Thuidium recognitum	.	.	.	.	.028	.072	.	.
Aulacomnium palustre	.	.	.	.	.600	.004	18.68	.108
Tomenthypnum nitens	.	.	.	.	.	.	31.88	.020
Sphagnum fuscum	.	.	.	.	.	.	1.35	.444
Sphagnum nemoreum	.	.	.	.	.	.	.700	.020
Sphagnum angustifolium	.	.	.	.	.	.	1.62	.060
Sphagnum russowii	.	.	.	.	.	.	.	.
Sphagnum warnstorfii	.	.	.	.	.	.	1.32	.300
Dicranum undulatum	.	.	.	.	.	.	.468	.388
Dicranum fuscum	.	.	.	.	.	.004	.	.
Drepanocladus revolvens	.	.	.	.	.	.	.328	.
Bryum pseudotriquetrum	.	.	.	.	.	.	.296	.020
Helodium blandowii	.	.	.	.	.	.	.060	.004
Polytrichum strictum	.	.	.	.	.	.	.	.
Orthotrichum speciosum	.	.	.	.	.	.	.	.
Amblystegium juratzkanum	.	.	.	.	.	.	.	.
Pohlia nutans	.	.004	.044	.012	.	.	.	.
Plagiomnium glabella	.	.	.004	.	.	.	.	.

continued ...

Table 5. Continued

GROWTH-FORM / *Species*	Reference Stand Number							
	Aeolian Sand H.T.				Glacial Till H.T.		Peatland H.T.	
	1	2	3	4	5	6	7	8
TERRESTRIAL LICHENS	*52.28*	*43.64*	*.388*	*.352*	*1.83*	*.412*	*3.66*	*2.81*
Cetraria ericetorum	.136	.092	.	.	.	.	.	.
Cetraria nivalis	.008	.004	.	.	.	.	.	.
Cladonia uncialis	.024	.072	.	.	.	.	.	.
Stereocaulon alpinum	.088	.024	.	.	.	.	.	.
Cladonia phyllophora	.172	.188	.	.	.	.	.	.
Cladonia pyxidata	.052	.004	.	.	.	.	.008	.
Peltigera malacea	.888	1.30	.	.	.	.	.100	.008
Cladonia coccifera	.248	.044	.	.	.	.	.008	.008
Cladina stellaris	.032	.256	.004	.	.	.	.	.
Cladina mitis	48.60	40.80	.080	.	.	.004	.848	1.47
Icmadophila ericetorum	.	.	.004	.	.	.	.004	.
Cetraria pinastri	.024	.	.	.	.	.008	.004	.
Cladonia cornuta	.132	.080	.016	.004	.	.008	.208	.044
Cladonia gonecha	.072	.004	.032	.	.	.	.008	.
Cladonia cristatella	.052	.004	.	.	.	.	.004	.
Cladonia crispata	.016	.	.	.	.	.	.	.
Cladonia subulata	.	.	.	.	.	.	.016	.
Cladonia furcata	.	.	.	.	.	.	.	.
Peltigera pulverulenta	.040	.	.	.036	.	.	.020	.080
Cladonia capitata	.008	.004	.	.	.	.	.	.
Leptogium saturninum	.	.	.	.	.	.	.	.
Peltigera horizontalis	.	.	.	.	.020	.	.	.
Peltigera polydactyla	.	.	.	.	.012	.116	.564	.024
Cladonia cenotea	.068	.	.016	.004	.004	.	.024	.004
Cladonia gracilis	.412	.124	.012	.008	.	.004	.316	.012

continued ...

Table 5. Concluded

GROWTH-FORM *Species*	Reference Stand Number							
	Aeolian Sand H.T.				Glacial Till H.T.		Peatland H.T.	
	1	2	3	4	5	6	7	8
Cladonia multiformis	.680	.336	.004	.008	.004	.004	.448	.012
Cladonia chlorophaea	.212	.048	.068	.092	.052	.068	.268	.088
Cladonia coniocraea	.040	.012	.092	.048	.016	.008	.	.008
Peltigera aphthosa	.152	.184	.020	.	.024	.	.600	.844
Peltigera rufescens	.116	.060	.040	.152	.168	.192	.204	.212
Cladina rangiferina	.004	.	.	.	.	.	.004	.
Cladonia verticillata	.004	.	.	.	.	.	.	.
Peltigera canina	.	.	.	.	.	.	.	.

[a] % cover of growth-forms was calculated as the sum of the mean % cover values of component species and printed in italicized numbers.

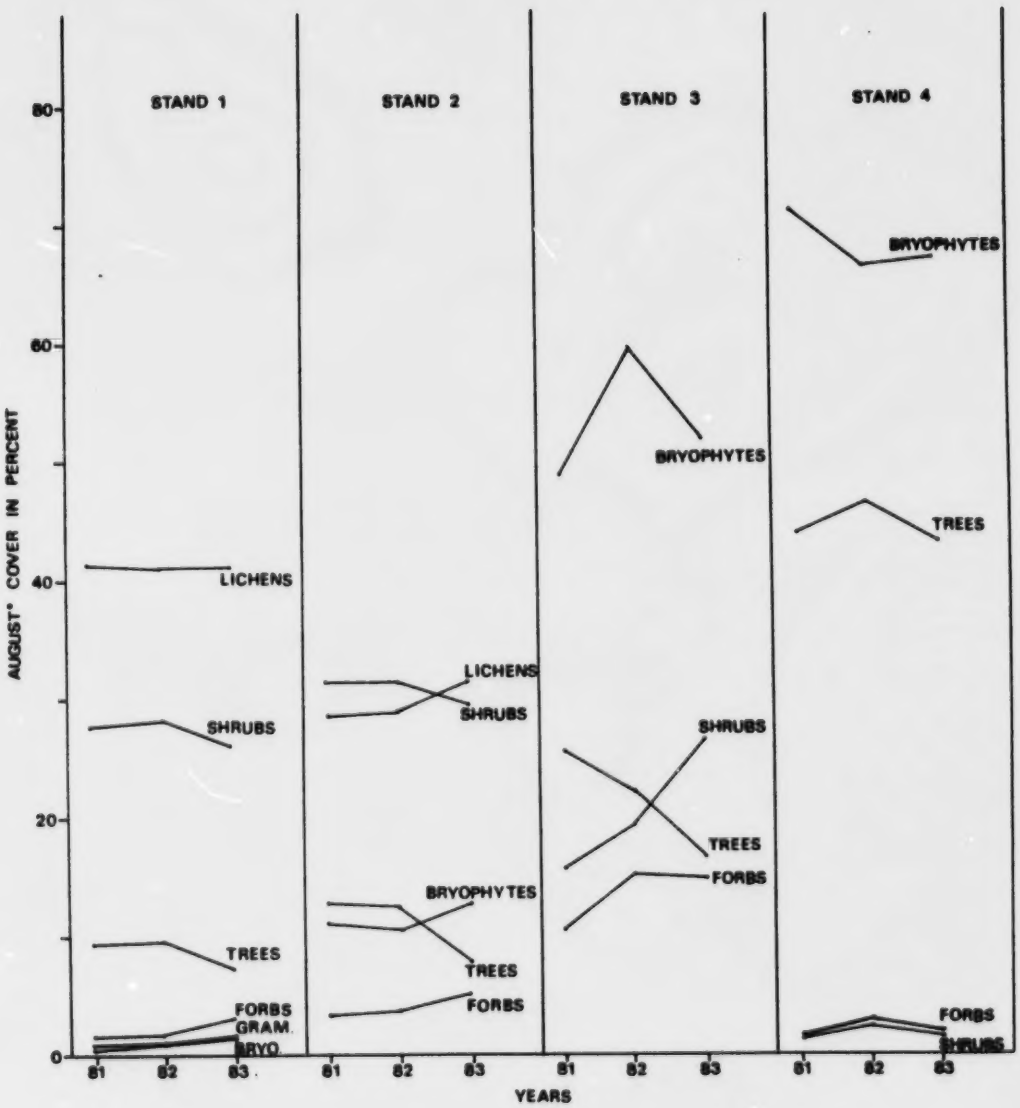
3.2.2 Annual Variation in Cover of Plant Growth-forms (1981-1983)

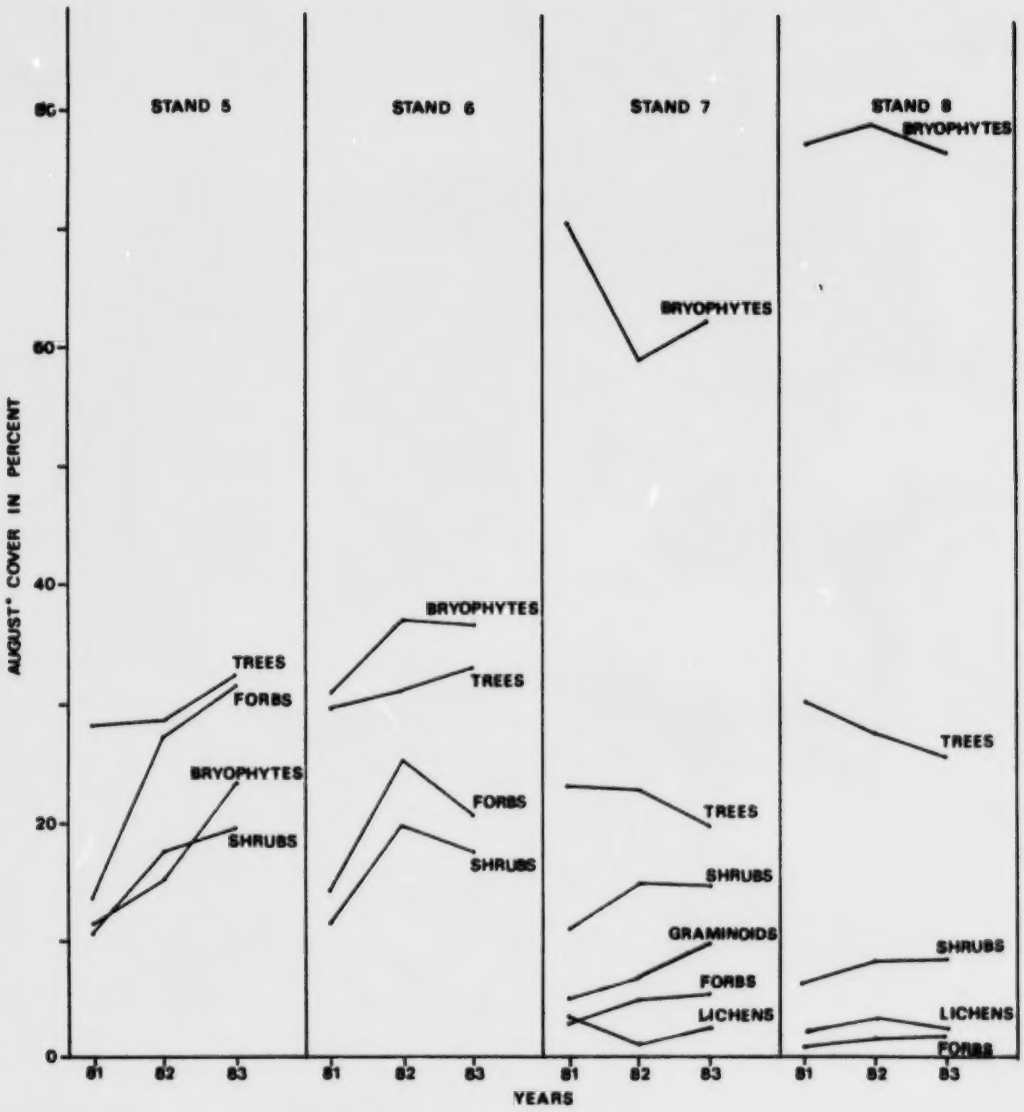
With only three years of data it is probably too early to infer specific environmental causes for changes in the cover of plant growth-forms. We will therefore simply describe graphically the annual variations observed between 1981, 1982, and 1983 (Figure 1). Large increases in forb and shrub cover in August 1982 over the previous year were generally tempered or reversed in 1983, although 1983 levels were still considerably above 1981. Stand no. 3 was the exception, in that shrub cover increased more in 1983 than in 1982.

There does appear to be a pattern of parallel responses of shrubs and forbs in stand nos. 4-8. In stand nos. 1 and 2, however, where total shrub cover consists primarily of mat-forming dwarf shrubs, competitive interactions among growth-forms may outweigh common responses to environment.

Some of the variations in cover of growth-forms between 1982 and 1983 (Figure 1) may be accountable to a change in staff making the monthly surveys of vascular plant communities (see also sections 2.5 above and 3.2.4 below); Robert Ellis was co-surveyor with George La Roi for the 1981 and 1982 surveys; in 1983 Ellis was succeeded by Michael Ross, who will also be co-surveyor in 1984.

Figure 1. Annual variations in percent cover of major plant growth-forms in the eight reference stands of the Hondo - Lesser Slave Lake study area of north central Alberta in 1981-83. Based on data from August surveys of the three years (see Table 5). Stand nos. 1, 2, 4 and 8 have generally varied less than have nos. 3, 5, 6 and 7.


STAND 1
STAND 2
STAND 3
STAND 4
AUGUST' COVER IN PERCENT
80
60
40
20
0
LICHENS
SHRUBS
TREES
FORBS
GRAM.
BRYO.
BRYOPHYTES
TREES
LICHENS
SHRUBS
BRYOPHYTES
TREES
FORBS
SHRUBS
TREES
FORBS
BRYOPHYTES
TREES
FORBS
SHRUBS
81
82
83
YEARS


STAND 5
STAND 6
STAND 7
STAND 8
80
60
40
20
0
AUGUST* COVER IN PERCENT
TREES
FORBS
BRYOPHYTES
SHRUBS
BRYOPHYTES
TREES
FORBS
SHRUBS
BRYOPHYTES
TREES
SHRUBS
GRAMINOIDS
FORBS
LICHENS
BRYOPHYTES
TREES
SHRUBS
LICHENS
FORBS
81
82
83
YEARS

3.2.3 Annual Variation in Plant Community Attributes (1981-1983)

Estimated total vascular plant cover decreased in six stands in 1983, and increased modestly in stand nos. 3 and 5 (Table 6). Species richness (*R*) showed little change in 1983, but evenness (*E*) and diversity (*H'*) increased significantly in stand nos. 1, 2, 3, and 7.

Total cover of bryophytes and lichens increased dramatically in four stands (nos. 2, 3, 6, and 7), but remained fairly constant in the other stands in 1983 (Table 7, Figure 1). The increases may be attributable to high precipitation amounts in June and July, 1983. However, high precipitation in July 1982 did not elicit a comparable increase in either bryophyte or lichen cover that year (see section 3.2.1). Species diversity of the bryoid stratum was also higher in August 1983 than in August 1982 in each of the eight stands; in seven stands the diversity increase was partially due to an increase in evenness, i.e. minor species were relatively more abundant in 1983 than in 1982.

Division of the total plant community into vascular plant and terrestrial bryoid (bryophyte + lichen) subcommunities permits some interesting comparisons of their attributes (*R*, *D*, *H'*, *E*). For example, evenness, which is independent of richness, is higher in the vascular plant subcommunity than it is in

Table 6. Comparison of August 1981, 1982, and 1983 vascular plant community attributes and vascular growth-form cover values of the eight SEADYN reference stands in the Hondo - Lesser Slave Lake area of north central Alberta.

Habitat Type[a]		PIGL [PIBA]				PIGL [POTR]		PIMA [LALA]	
Reference Stand Number		1	2	3	4	5	6	7	8
Community Attribute[b]	Year								
Total Cover (%)	1981	40.3	48.7	53.3	47.2	53.0	56.7	42.9	38.4
	1982	41.0	48.4	58.5	51.8	73.9	77.1	49.6	38.7
	1983	38.6	43.4	60.1	45.1	76.3	73.9	47.8	36.7
Species Richness (R)	1981	41	40	49	39	41	54	40	34
	1982	42	39	45	38	45	55	41	33
	1983	42	39	44	37	44	54	40	36
Dominance Index (D)	1981	0.28	0.19	0.23	0.39	0.17	0.12	0.28	0.63
	1982	0.26	0.17	0.17	0.34	0.13	0.09	0.22	0.52
	1983	0.21	0.15	0.13	0.37	0.12	0.10	0.17	0.50
Diversity Index (H')	1981	1.76	2.08	2.07	1.29	2.32	2.57	1.98	0.92
	1982	1.81	2.15	2.27	1.50	2.52	2.72	2.15	1.22
	1983	2.09	2.33	2.46	1.39	2.50	2.69	2.31	1.25
Evenness Index (E)	1981	0.47	0.56	0.53	0.35	0.63	0.64	0.54	0.26
	1982	0.48	0.59	0.60	0.41	0.66	0.68	0.58	0.35
	1983	0.56	0.64	0.65	0.39	0.66	0.67	0.63	0.35

[a] Full names and descriptions of habitat types in section 3.1 of First Report.

[b] Community attributes defined in section 1.2 of First Report.

Table 7. Comparison of June 1981, August 1982, and August 1983 terrestrial bryophyte and lichen community attributes of the eight SEADYN reference stands in the Hondo - Lesser Slave Lake area of north central Alberta.

Habitat Type[a]		PIGL [PIBA]				PIGL [POTR]		PIMA [LALA]	
Reference Stand Number		1	2	3	4	5	6	7	8
Community Attribute[b]	Year								
Total Cover (%)	1981	52.9	45.0	64.1	69.6	9.0	16.4	73.7	79.4
	1982	55.5	44.4	44.4	63.2	9.5	34.2	51.9	81.7
	1983	59.2	56.8	66.3	62.5	8.7	48.3	63.2	79.2
Species Richness (R)	1981	31	27	22	22	21	23	37	28
	1982	34	35	21	24	22	22	33	30
	1983	36	39	24	20	20	22	34	29
Dominance Index (D)	1981	0.71	0.65	0.59	0.37	0.23	0.21	0.31	0.46
	1982	0.74	0.64	0.48	0.39	0.22	0.26	0.41	0.49
	1983	9.68	0.56	0.51	0.38	0.21	0.23	0.34	0.44
Diversity Index (H')	1981	0.79	0.80	0.84	1.13	1.76	1.79	1.54	1.01
	1982	0.62	0.83	0.95	1.07	1.73	1.56	1.20	0.95
	1983	0.86	0.97	0.96	1.16	1.86	1.66	1.57	1.03
Evenness Index (E)	1981	0.23	0.24	0.27	0.37	0.37	0.57	0.43	0.30
	1982	0.18	0.23	0.31	0.34	0.34	0.50	0.34	0.28
	1983	0.24	0.28	0.30	0.39	0.39	0.54	0.44	0.31

[a] Full names and descriptions of habitat types in section 3.1 of First Report.

[b] Community attributes defined in section 1.2 of First Report.

the bryoid subcommunity in all eight stands. Perhaps this pattern reflects a limitation in the opportunity for niche partitioning among terrestrial bryophytes and lichens cf. vasculars, which are vertically segregated into three distinct strata. A "fairer" comparison would include abundance data on epiphytic bryophytes and lichens; as yet we do not have such data, however.

3.2.4 Comparison of Quadrat and Line-Intercept Methods of Estimating Species Cover

Four times during the summer of 1983 shoot/thallus cover was estimated concurrently in the eight reference stands by both quadrat and line-intercept methods (see section 2.5). Table 8 compares the results of the two techniques for stand no. 3, a mature *Pinus banksiana* stand, in early August. In general, there is close agreement between methods.

For vascular species, the line-intercept estimates are very similar to those of the more intensive quadrat survey, with little evidence of bias associated with plant growth-form. Two disadvantages of the line-intercept method are (1) a moderate increase in the variability of estimates for most vascular species, and (2) a tendency to under-sample relatively rare or restricted species. For example, four species which had 2% cover or more in at least one 5x5 m quadrat but which were relatively restricted in distribution in the general area (*Ledum groenlandicum*, *Viola renifolia*, *Dryopteris*

Table 8. Percent cover estimates for plant species[a] recorded at least once[b] by both the line-intercept (LI) and quadrat (Q) survey methods in reference stand no. 3 on 3 August 1983.

Plant Species Code Name[a]	Mean Cover (%)		Cover Rank[c]		Coefficient of Variation (st. dev./mean)	
	Q	LI	Q	LI	Q	LI
Vasculars						
ALCR	11.68	9.44	1	2	0.54	0.79
ARNU	10.08	9.91	2	1	0.30	0.35
LIBO	5.12	5.97	3	3	0.72	0.70
MACA	2.68	2.47	4	6	0.56	0.94
VAVI	2.10	1.36	5	10	0.86	0.88
ROAC	2.06	2.69	6	5	0.58	1.10
VAMY	1.74	1.77	7	8	0.68	0.97
RUID	1.65	1.83	8	7	1.01	1.89
COCA	1.26	2.98	9	4	2.12	2.38
PRPE	0.88	0.21	10	15	1.99	3.16
ARUV	0.82	1.46	11	9	2.46	1.52
ELIN	0.56	1.06	12	11	0.57	1.13
RUPU	0.37	0.24	13	14	1.91	3.16
EPAN	0.36	0.38	14	12	1.88	3.17
LYCO	0.34	0.04	15	19	2.32	3.17
ORSE	0.33	0.04	16	18	1.41	2.27
GABO	0.07	0.33	17	13	1.51	1.99
SCPU	0.02	0.08	18	17	5.00	3.16
GELI	0.01	0.08	19	16	4.00	3.17
ORAS	0.0004	0.03	20	20	5.00	3.17
Bryoids						
PLESCH	34.88	53.49	1	1	0.67	0.43
HYLSPL	8.74	3.50	2	2	1.38	1.66
PTIC-C	6.04	6.16	3	3	2.57	1.79
DICPOL	0.98	0.72	4	4	1.56	1.67

[a] Vascular species code names are derived from the first two letters of the genus and species names; bryoid species code names are derived from the first three letters of the genus and species names.

[b] Seventeen vascular and 7 bryoid species were recorded in quadrat but not in line-intercept surveys; 4 bryoid species were recorded in line-intercept but not quadrat surveys.

[c] Cover rankings are for those species recorded at least once in both surveys.

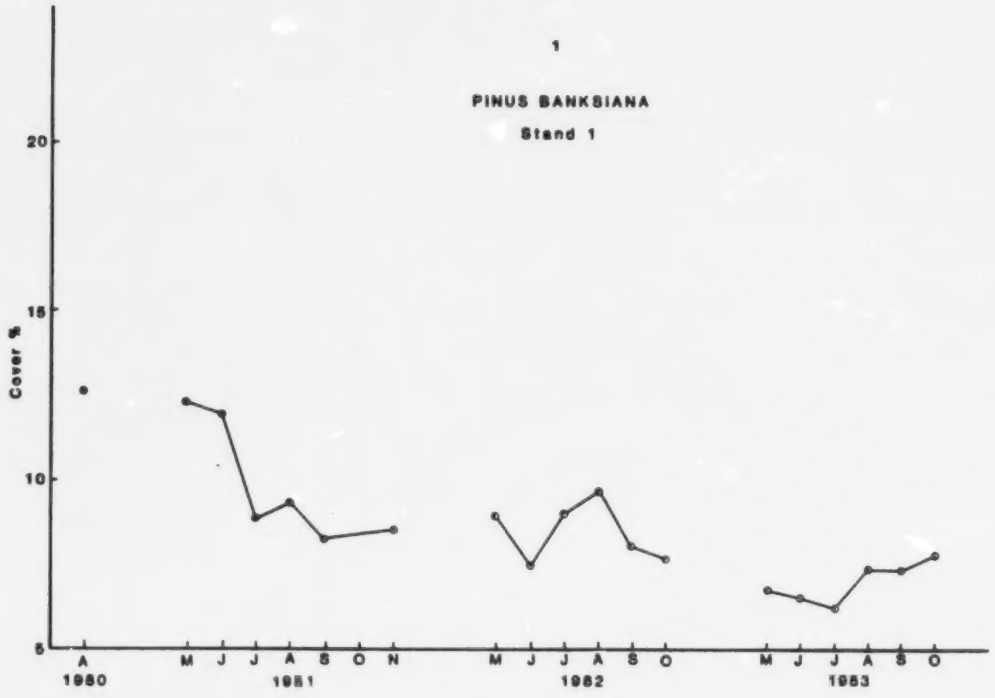
carthusiana and *Lycopodium annotinum*) were unrecorded in the line-intercept survey. However, the line-intercept method documents monthly changes in cover of the major vascular understory species very adequately.

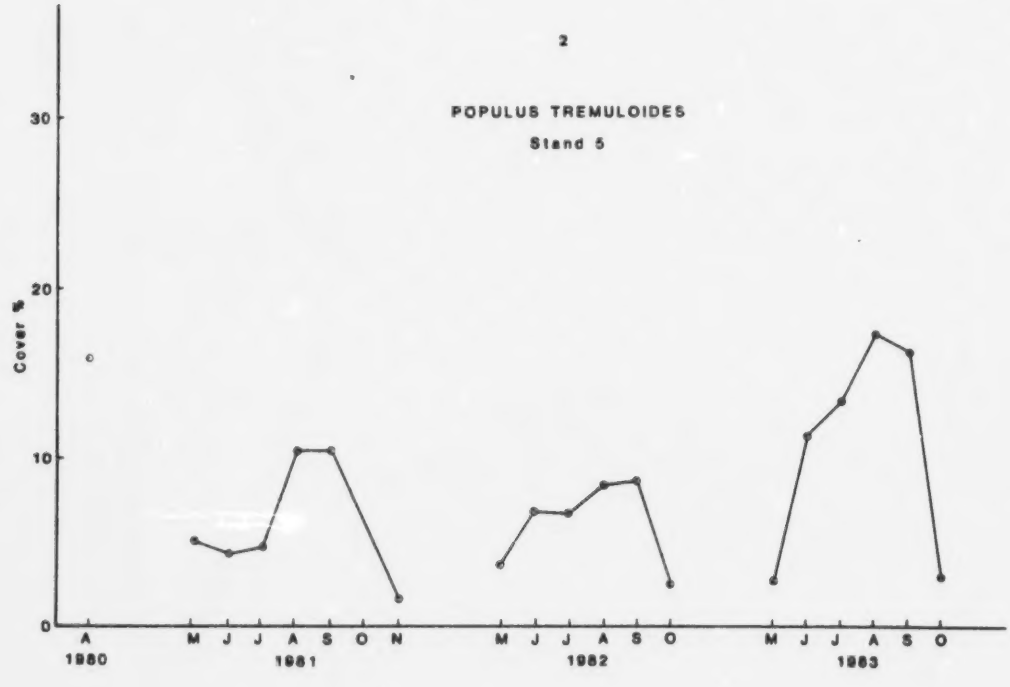
The line-intercept method also seems well-suited to sampling bryophyte and lichen species. For two of the three leading bryophyte species, line-intercept estimates show considerably less variation than those from the 0.5 sq m quadrats (Table 8). Furthermore, nearly as many species (4) appeared only in the line-intercept surveys as were recorded only in quadrats (7). The discrepancy between the cover estimates for *Hylocomium splendens* may simply be a function of the clumped dispersion of that species in stand no. 3. In contrast, *Pleurozium schreberi* is probably more abundant on the edges of the stand, where the line transects were established, than in the center of the stand.

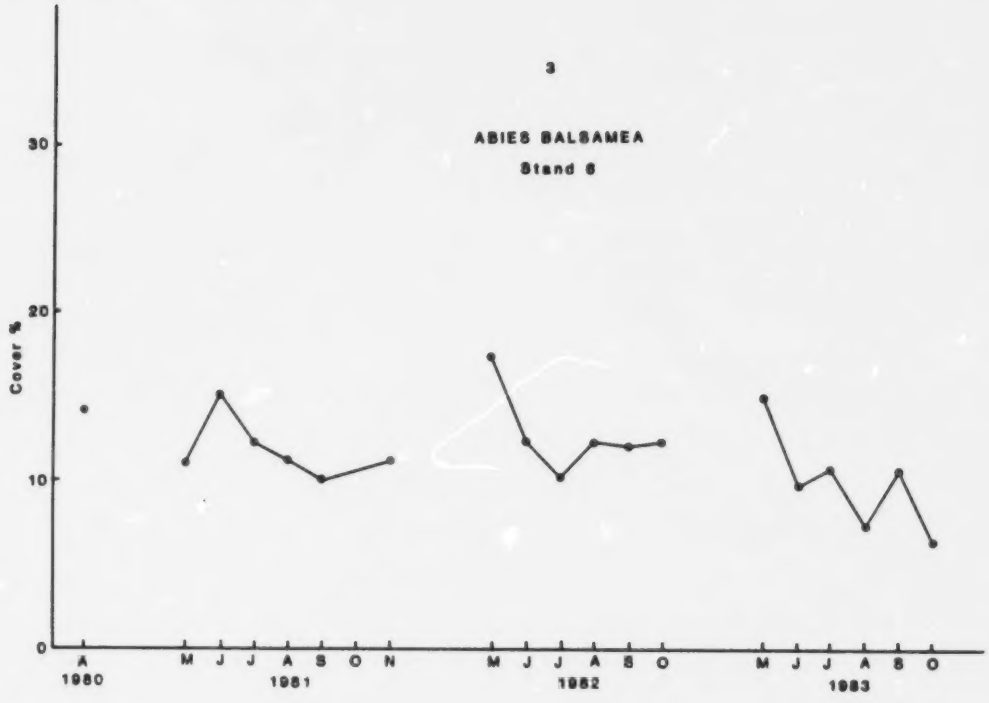
3.3 SHOOT COVER DYNAMICS OF PLANT SPECIES POPULATIONS DURING 1981-1983

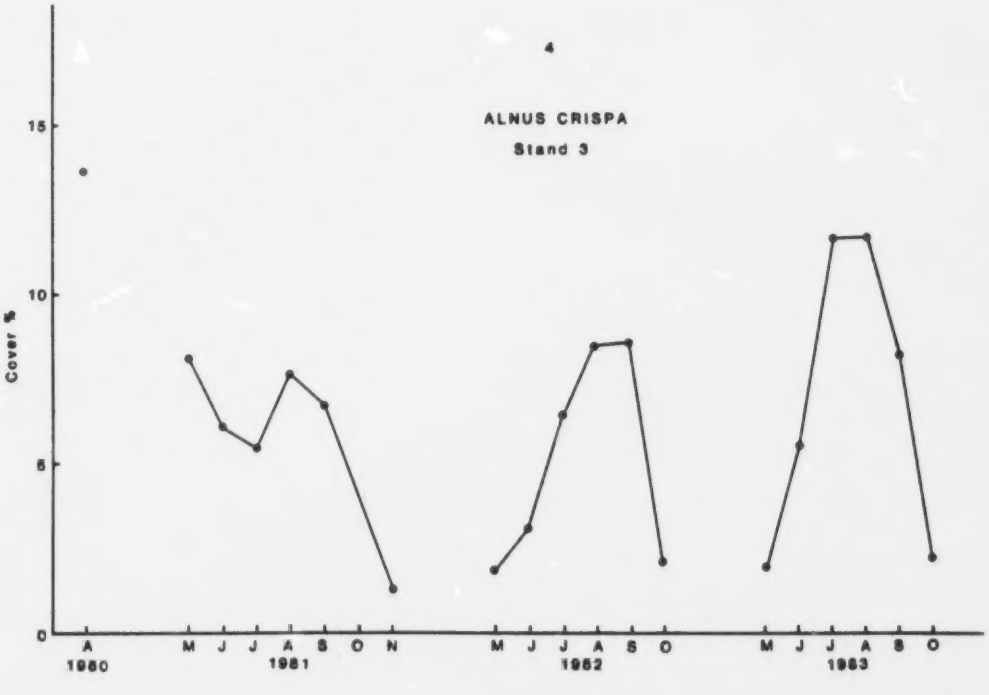
With the completion of a third full snow-free season in which cover was estimated monthly in permanent quadrats, characteristic patterns of dynamic behavior have begun to emerge, especially for vascular plant species. The patterns depicted in Figure 2 not only suggest strategies evolved by species with regard to the production and maintenance of photosynthetic tissue, but may also provide reasonable calibrations for vegetation

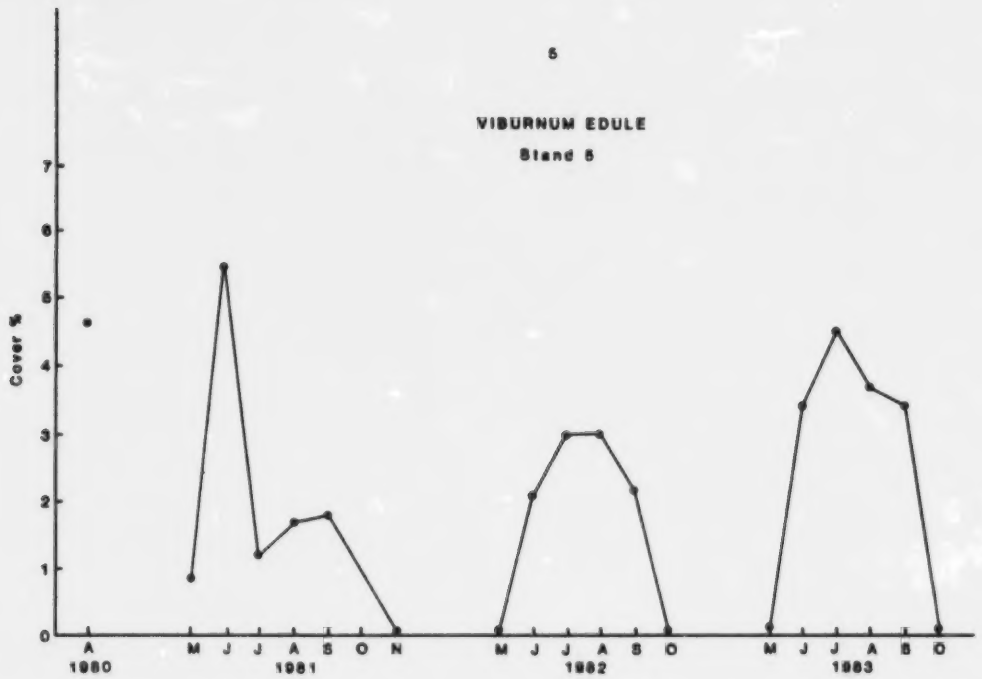
Figure 2. Shoot/thallus cover dynamics of selected plant species populations in selected SEADYN reference stands in 1981, 1982, and 1983. See also Figure 5 in First Report and Figure 1 in Second Report.

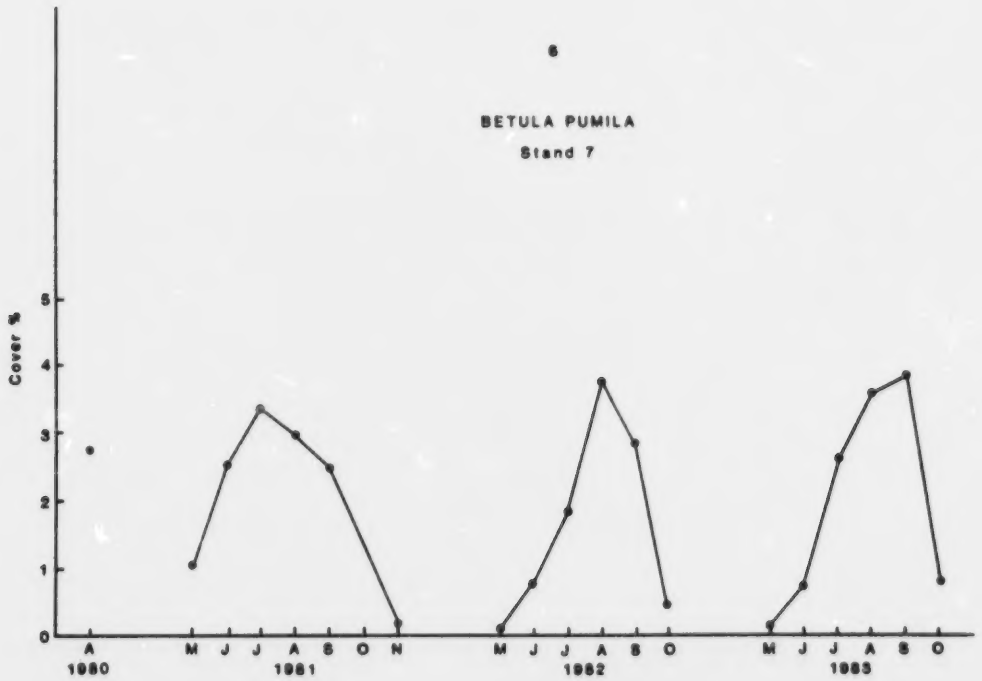

1
PINUS BANKSIANA
Stand 1
Cover %
20
15
10
5
A
M J J A S O N
M J J A S O
M J J A S O
1980
1981
1982
1983


2
POPULUS TREMULOIDES
Stand 5
Cover %
30
20
10
0
A
M J J A S O N
M J J A S O
M J J A S O
1980
1981
1982
1983


3
ABIES BALSAMEA
Stand 6
Cover %
30
20
10
0
A
1980
M J J A S O N
1981
M J J A S O
1982
M J J A S O
1983


4
ALNUS CRISPA
Stand 3
Cover %
15
10
5
0
A
1980
M J J A S O N
1981
M J J A S O
1982
M J J A S O
1983

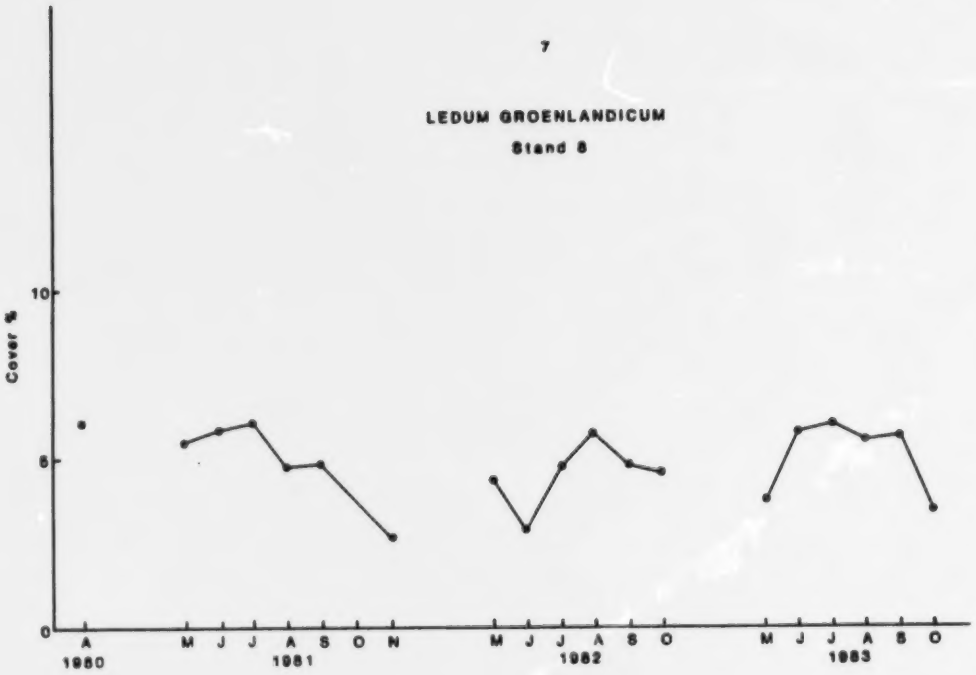

5
VIBURNUM EDULE
Stand 5
Cover %
0
1
2
3
4
5
6
7
A
M J J A S O N
M J J A S O
M J J A S O
1980
1981
1982
1983


6
BETULA PUMILA
Stand 7
Cover %
0
1
2
3
4
5
A
M J J A S O N
M J J A S O
M J J A S O
1980
1981
1982
1983

7

LEDUM GROENLANDICUM

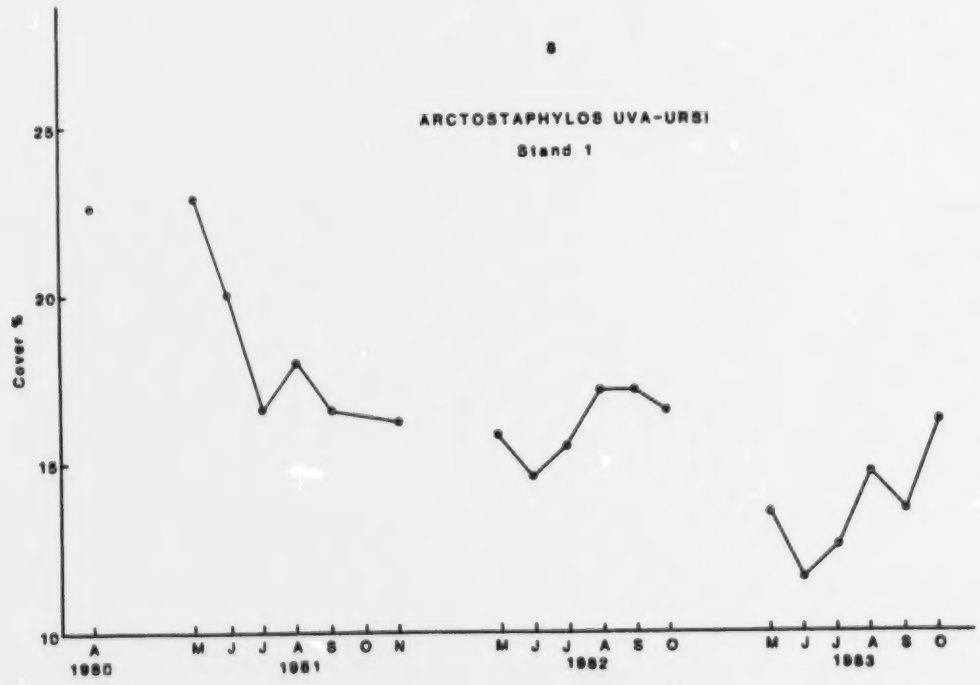
Stand 8

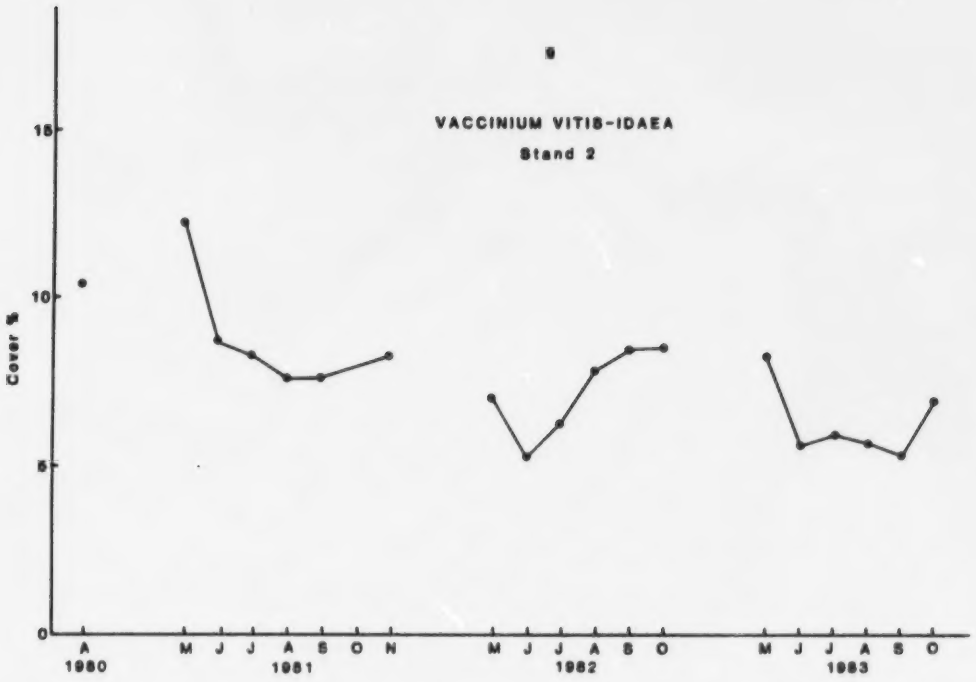


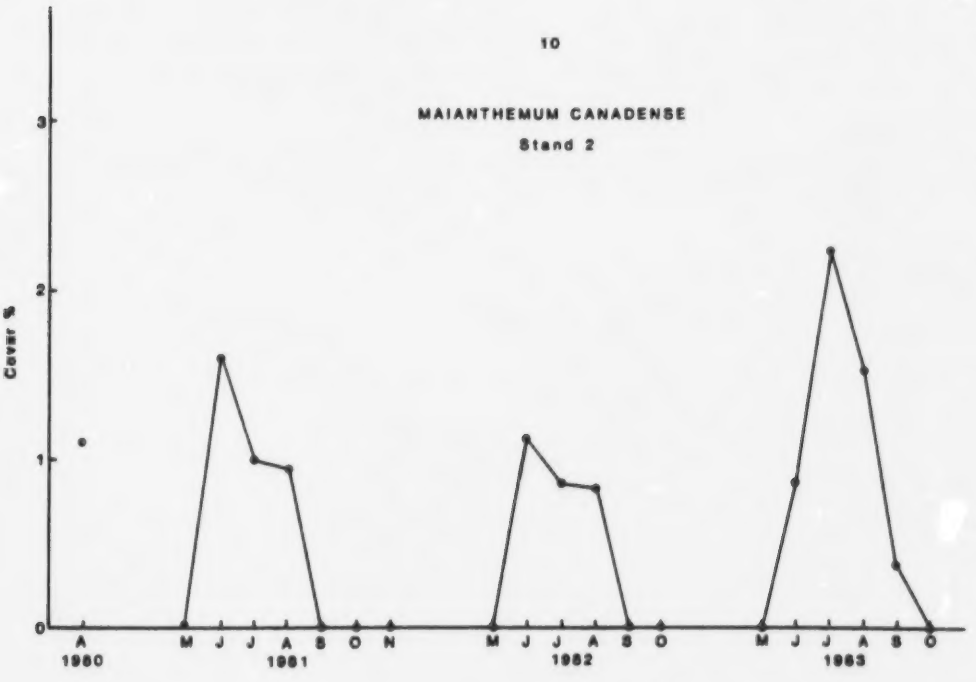
8

ARCTOSTAPHYLOS UVA-URSI

Stand 1



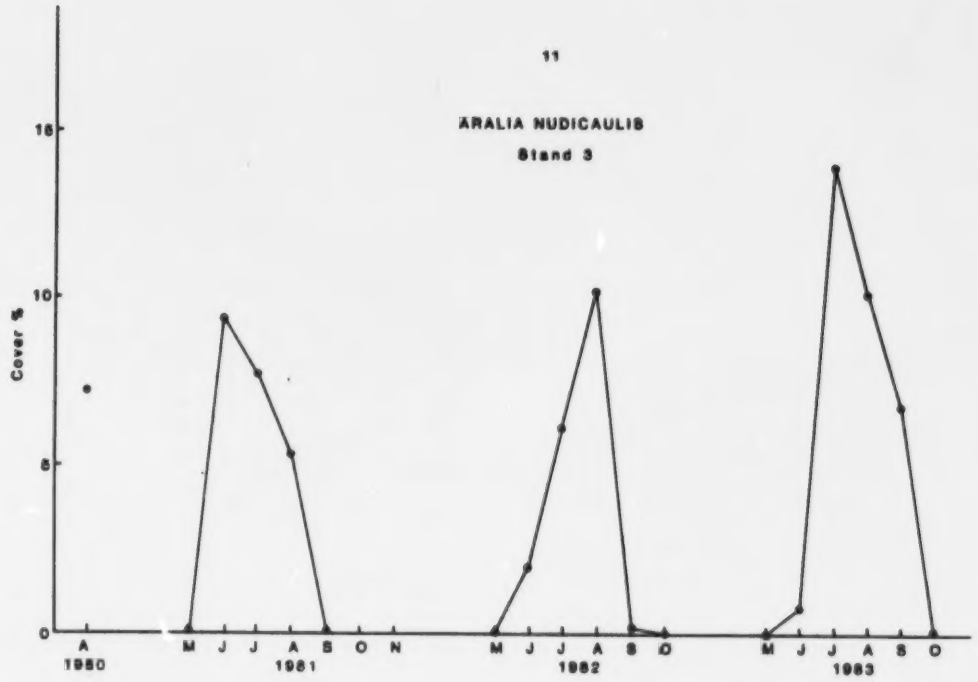

VACCINIUM VITIS-IDAEA
Stand 2
Cover %
15
10
5
0
A
1980
M J J A S O N
1981
M J J A S O
1982
M J J A S O
1983


MAIANTHEMUM CANADENSE
Stand 2
Cover %
3
2
1
0
A
1980
M J J A S O N
1981
M J J A S O
1982
M J J A S O
1983

11

ARALIA NUDICAULIS

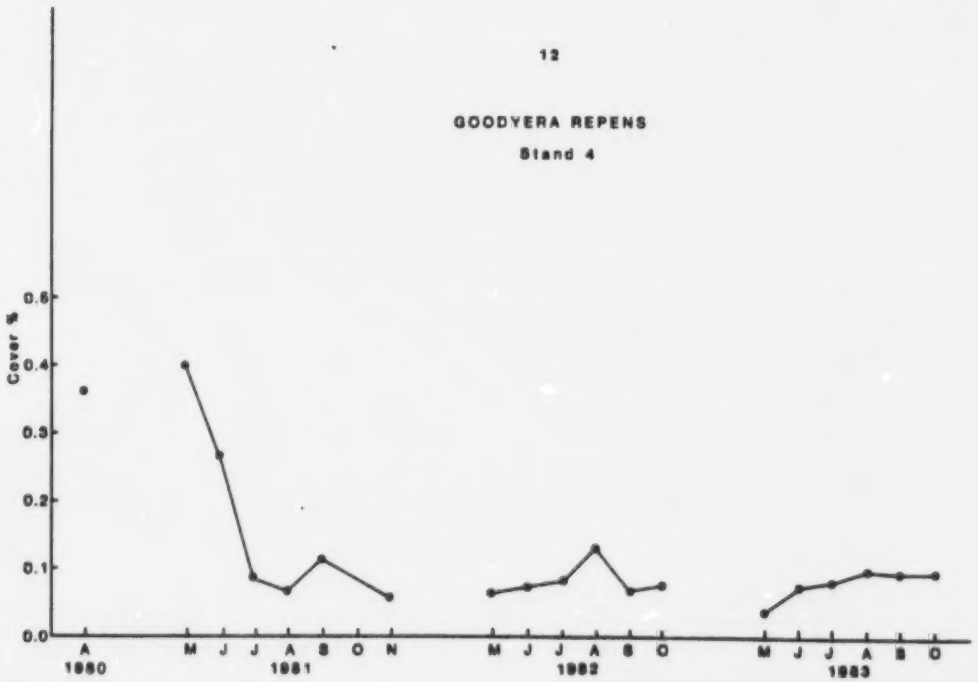
Stand 3



12

GOODYERA REPENS

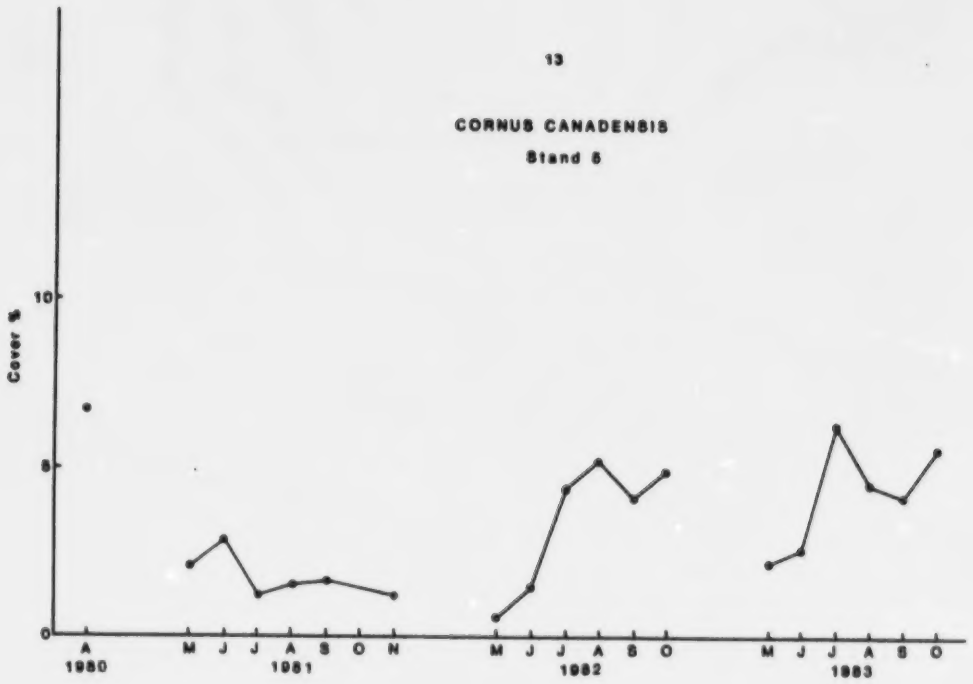
Stand 4



13

CORNUS CANADENSIS

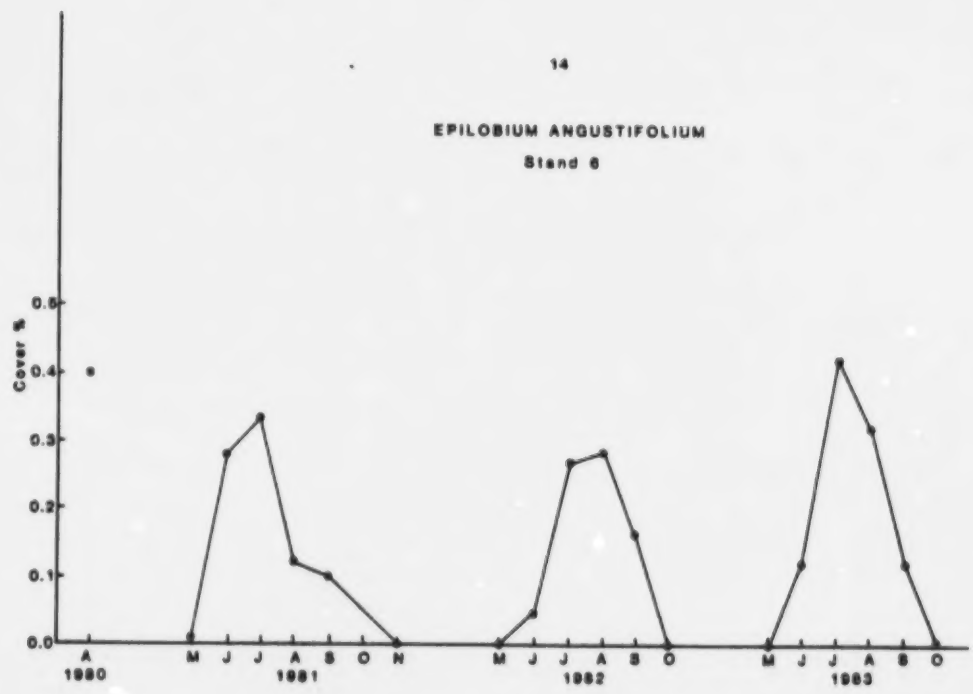
Stand 6



14

EPILOBIUM ANGUSTIFOLIUM

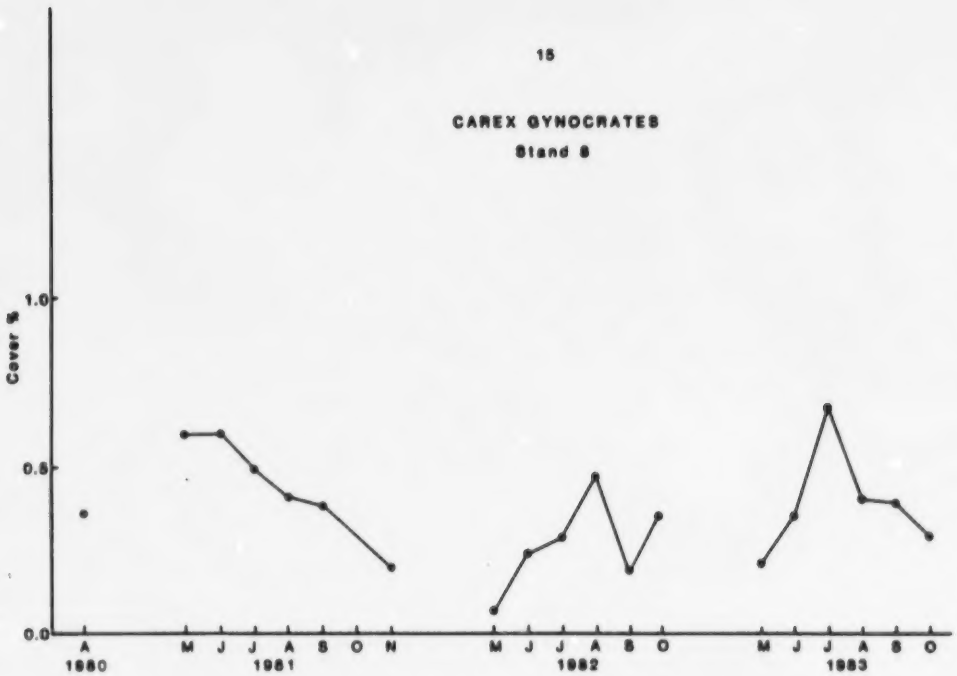
Stand 6



15

CAREX GYNOCRATES

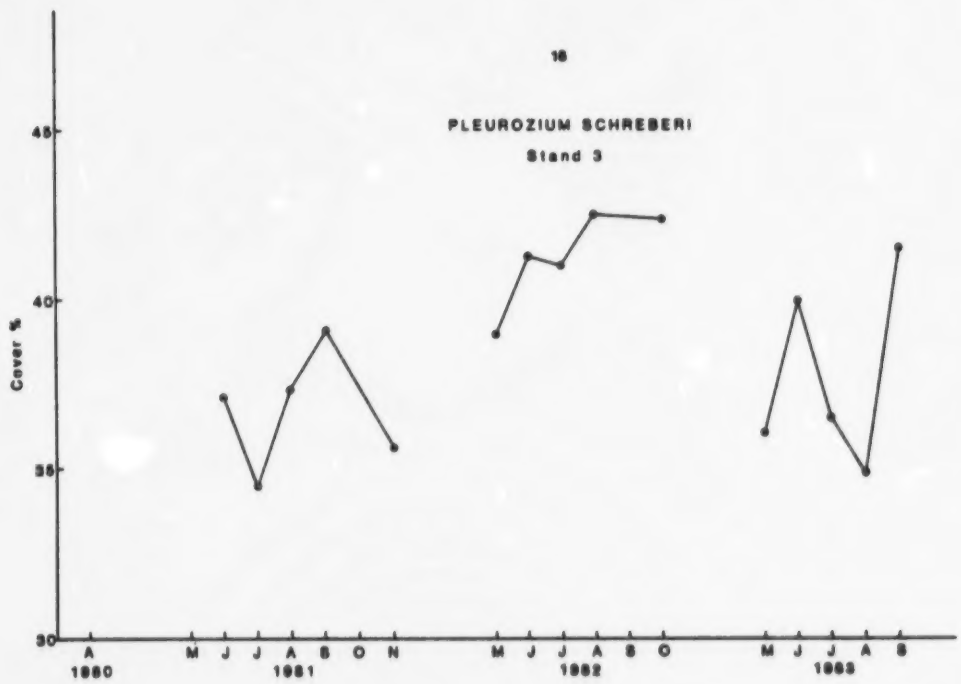
Stand 8



16

PLEUROZIUM SCHREBERI

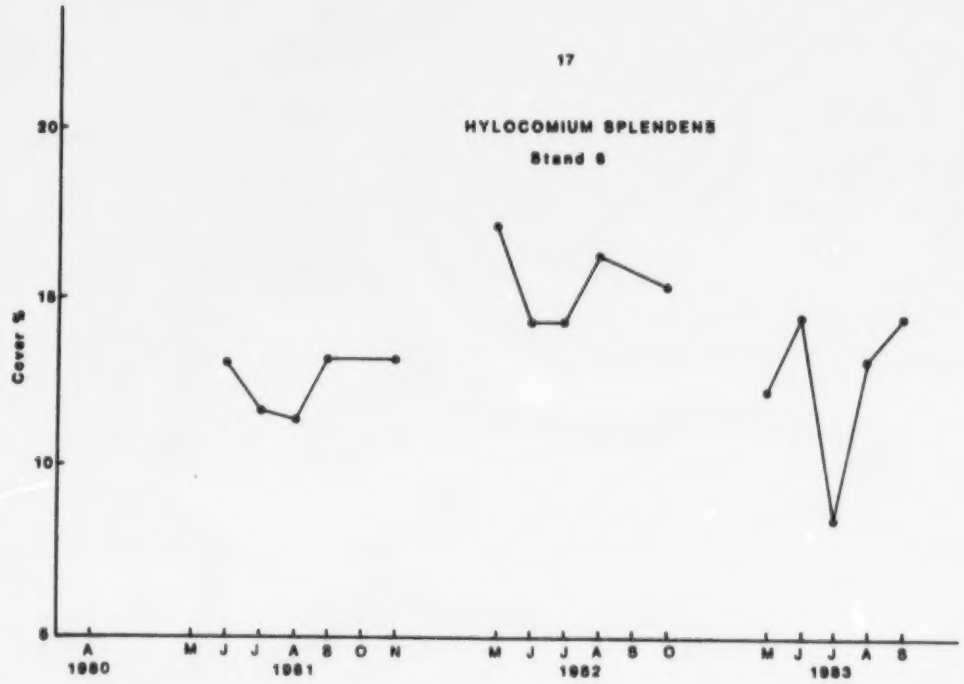
Stand 3



17

HYLOCOMIUM SPLENDENS

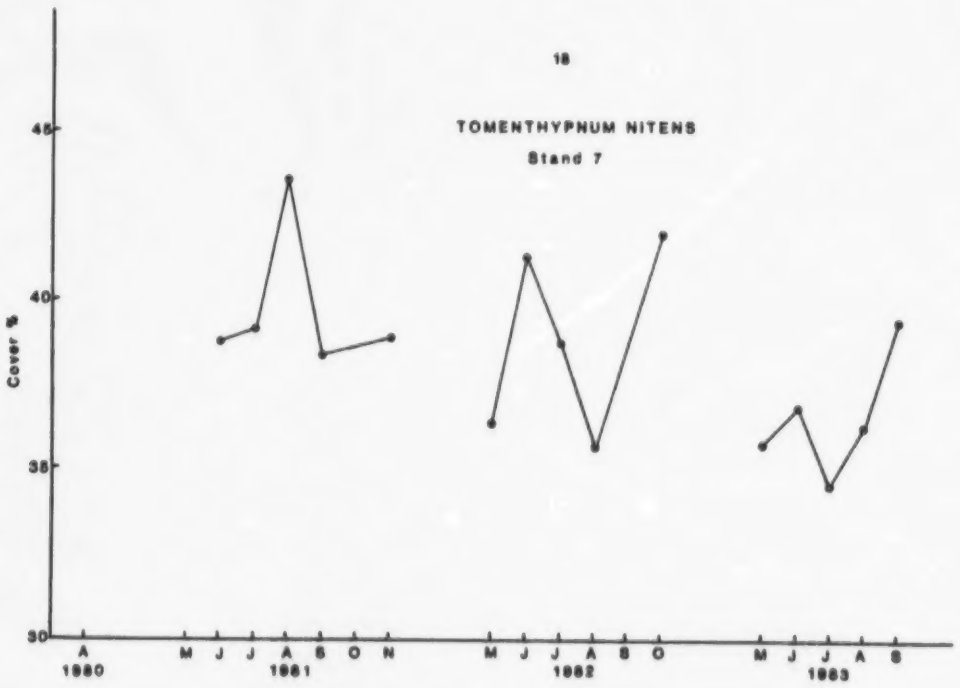
Stand 6

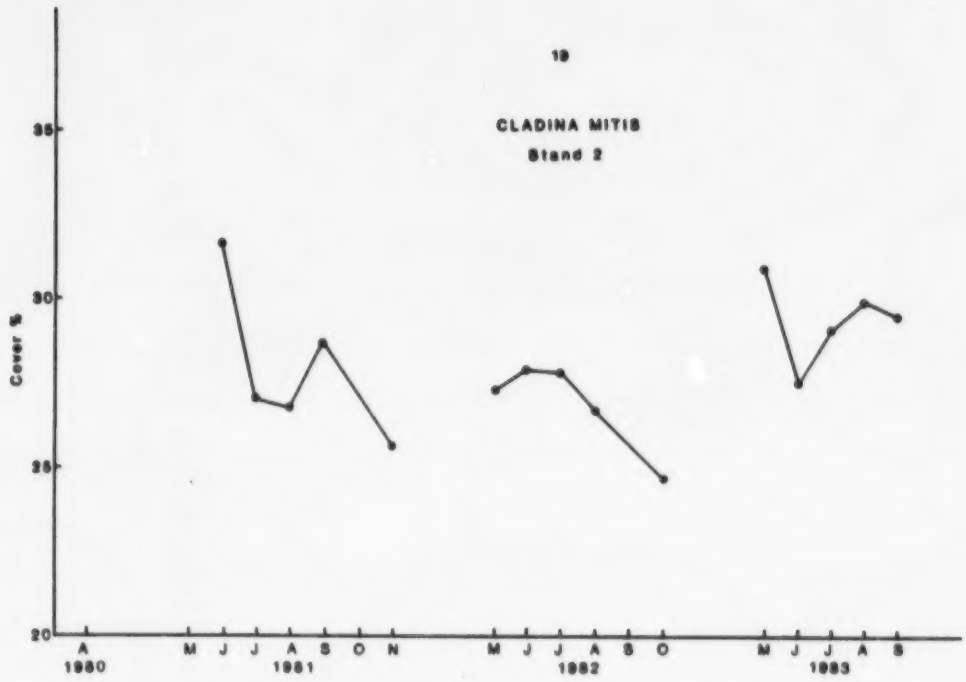


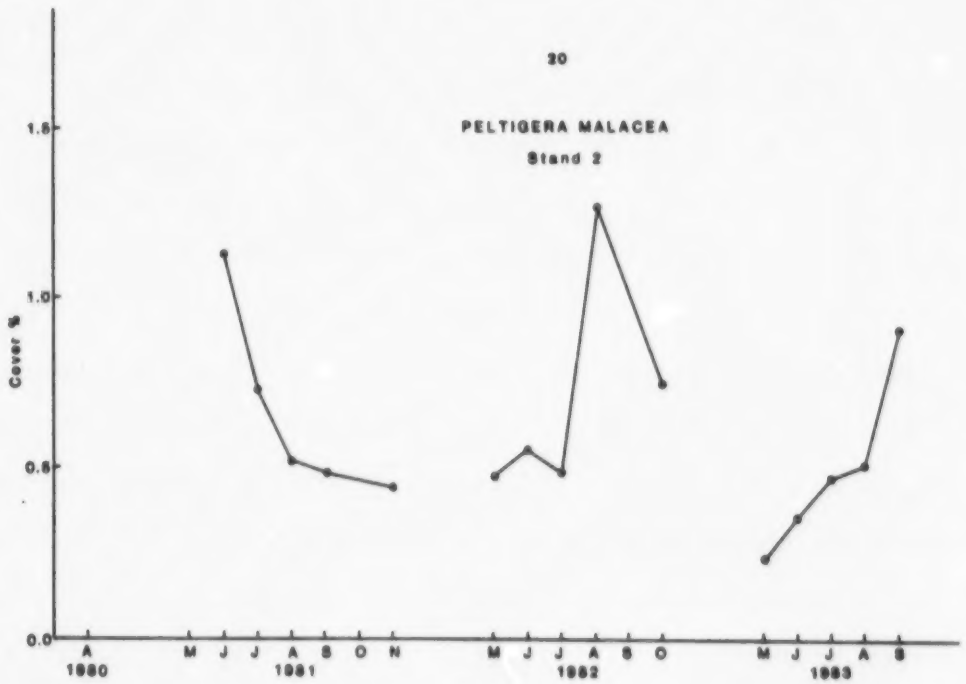
18

TOMENTHYPNUM NITENS

Stand 7




19
CLADINA MITIS
Stand 2
Cover %
35
30
25
20
A
M J J A S O N
M J J A S O
M J J A S
1980
1981
1982
1983


20
PELTIGERA MALACEA
Stand 2
Cover %
1.5
1.0
0.5
0.0
A
M J J A S O N
M J J A S O
M J J A S
1980
1981
1982
1983

surveys taken at different times during the growing season in boreal forests (see First Report, section 1.1, page 3).

3.3.1 Vascular Species

A useful way to characterize the fluctuations in cover for vascular species (Figure 2, nos. 1-15) is to note the timing and duration of conspicuous peaks or sharp declines in shoot cover. Deciduous trees and shrubs (e.g., *Populus tremuloides*, *Alnus crispa*, *Viburnum edule*, *Betula pumila*) tend to have a broad plateau in shoot cover; although they may not reach maximum cover until August, they produce leaves early and maintain a substantial leaf area through most of the summer. The curves for the first three above-noted species illustrate the immediate impact of tent caterpillar defoliation in 1981, and a gradual recovery over the next two years.

Herbaceous perennials (e.g., *Maianthemum canadense*, *Aralia nudicaulis*, *Epilobium angustifolium*) usually have narrower, more peaked distributions. Compared to other growth-forms in the boreal forest, these plants produce and mature most of their leaves very rapidly when growing conditions become favorable, then steadily assimilate and store energy for the balance of the "photosynthetic season". Of course, not all herbaceous perennials fit this generalization; some are similar to deciduous shrubs in having either a protracted period of leaf production (e.g., *Fragaria virginiana*, not

shown) or long leaf longevity (e.g., *Mertensia paniculata*, *Aster laevis*, not shown). Of the herbs pictured in Figure 2, *Aralia* appears to be the most ephemeral within the annual cycle, while *Epilobium* is the most persistent. With regard to the timing of maximum shoot cover, *Aralia* and *Epilobium* were earlier in 1983 than 1982, while *Malanthemum* developed later. The annual variation in this characteristic indicates that (1) considerable environmental control is exerted over the typical developmental sequence for a particular species, and (2) not all species respond equally to this control.

Our surveys show that evergreen dwarf shrubs (e.g., *Arctostaphylos uva-ursi*, *Vaccinium vitis-idaea*) decrease in shoot cover early in the summer, then gradually recover to peak shoot cover late in the snow-free season. This pattern is consistent with observations of individual populations of these species, which begin to suffer noticeable leaf mortality in early June, but do not produce new leaves until mid- or late June. A similar early-season dip in shoot cover was observed for *Pinus banksiana*; its new needles typically elongate in early July. A June pulse of needle fall has been reported in several *P. banksiana* reference stands in the Athabasca Oil Sands study area north of Fort McMurray (La Roi 1984).

In contrast, *Ledum groenlandicum*, a low evergreen shrub, behaved more like a deciduous shrub than

the dwarf evergreen shrubs in 1983, with a June increase in cover, followed by a broad plateau, and an October decrease. Although new leaves are not produced by *Ledum* until late June, its reflexed overwintering leaves become more horizontal in orientation with warming temperatures in May, hence increasing its shoot cover (see section 4.5.1, page 102, First Report). Leaf senescence in this species occurs throughout the summer, and may cause a decrease in cover early in the season (Figure 2, no. 7, June 1982), but in monitored populations in 1983 most leaf mortality was concentrated in late summer.

Cornus canadensis, a wintergreen forb which was considerably reduced by tent caterpillar activity in 1981, increased abruptly in cover in July of 1982 and 1983. In this species, expansion of young leaves in mid-June coincided closely with senescence of surviving leaves of the previous year's cohort.

The pattern for perennial graminoids, as represented by *Carex gynocrates*, is not unlike that of perennial forbs; both growth-forms exhibit a sharp and conspicuous mid-summer peak in cover. Of course, wintergreen species such as *C. gynocrates* maintain some green tissue throughout the year.

3.3.2 Bryophyte and Lichen Species

In comparison to those of the vascular plants, annual cycles of bryophyte and lichen species cover are not obvious after three seasons of monthly surveys in 0.5

sq m microplots (Figure 2, nos. 16-20). The lichens, in particular, seem to lack a characteristic intraseasonal sequence.

Cladina mitis had a mid-summer cover trough in 1981, an autumn low in 1982, and an early summer trough in 1983. *Peltigera malacea* cover decreased at a decreasing rate in 1981, fluctuated greatly late in the 1982 season, and increased steadily throughout 1983. Judging from the monthly meteorological data from the three years presented in Section 3.1, these patterns are not related in any simple way to moisture stress, but it is true that the latter half-summers of 1982 and 1983 were much wetter than that of 1981, which would permit more growth by *P. malacea*. Also, lichen cover may increase/decrease greatly even on a daily basis depending on thallus swelling/shrinking during wetting/drying cycles. Such short-term variation may mask intraseasonal trends based on monthly surveys.

Bryophytes seem to respond in a more predictable manner to moisture stress than lichens. With the notable exception of *Tomenthypnum nitens* in 1981, the species response patterns shown in Figure 2 include a mid-summer dip in cover. However, species and stands differ in the timing of this mid-summer low. For instance, after an extremely wet July 1983, the cover of *Hylocomium splendens* in stand no. 6 and *Tomenthypnum nitens* in stand no. 7 returned to early June levels by 3 August, while

Pleurozium schreberi in stand no. 3 did not recover until September.

Just as for vascular plants, changes in cover of bryophytes and lichens are the net result of expansions and contractions of existing populations, and establishment/extinction of new/old ones. To understand the seasonal dynamics of these small plants, examination of individual populations is necessary. The next section describes some preliminary results of such a close-up study.

3.4 GROWTH RATES OF BRYOPHYTES AND LICHENS

Using the "cranked wire" technique of Clymo (1970) described by Busby (1976), the height growth rates of tagged populations of the three most abundant terrestrial bryophyte or lichen species in each reference stand were measured at monthly intervals during the snow-free season in 1982 and 1983. These measurements will continue in 1984 and 1985. Some preliminary results are given below.

3.4.1 Total Growth in 1983

Based on data from May to September 1983 (Table 9) *Pleurozium schreberi* showed a mean height growth increment of 14.5 mm (n = 7 populations) for the period of observation. Most of the stands yielded growth of 10-12 mm but stand nos. 5 and 6 had growth of 24.8 and 20.4 mm, respectively. Thus *P. schreberi* appears to be

Table 9. Height growth of terrestrial bryophytes and lichens in reference stands of the Hondo - Lesser Slave Lake study area in 1983. Mean values calculated from monthly measurements (mm) on tagged populations using the method of Clymo (1970) and Busby (1976).

BRYOID GROUP Species (n)*	Survey Month					1983 Total
	May	Jun	Jul	Aug	Sep	
FEATHER MOSSES						
Pleurozium schreberi (n = 7)	0	-2.14	7.31	6.49	2.83	14.49
Hylocomium splendens (n = 5)	0	-2.04	7.06	1.48	0.68	7.88
Ptilium crista-castrensis (n = 3)	0	-5.13	7.40	3.33	0.93	6.53
WETLAND MOSSES						
Sphagnum angustifolium (n = 1)	0	0.3	5.7	12.2	2.5	20.7
Sphagnum warnstorfii (n = 1)	0	4.2	4.4	5.2	5.4	19.2
Tomenthypnum nitens (n = 1)	0	2.4	0.8	1.0	5.2	9.4
Aulacomnium palustre (n = 1)	0	3.8	3.4	-1.2	2.8	8.8
POPLAR FOREST MOSSES						
Brachythecium salebrosum (n = 1)	0	-1.0	2.0	0.6	10.2	11.8
Plagiomnium cuspidatum (n = 1)	0	-4.8	8.6	0.6	-0.8	3.6
PINE WOODLAND LICHENS						
Cladina mitis (n = 3)	0	0.6	-0.9	0.7	-1.3	-0.4
Peltigera malacea (n = 1)	0	-1.2	1.4	-0.4	-0.2	-0.4

* n = number of tagged populations; five individuals are measured in each tagged population.

growing about twice as fast in stands of the *Picea glauca/Aralia nudicaulis* h.t. as it is in those of the other two habitat types.

Hylocomium splendens had a mean growth increment of 7.9 mm (n = 5) and showed a growth pattern similar to that of *P. schreberi*. Its maximum growth occurred in stand no. 6 (16.2 mm) and its minimum growth occurred in stand no. 8 (3.6 mm) under a dense canopy of *Picea mariana*.

Ptilium crista-castrensis was measured in stand nos. 3, 4, and 6, the latter two stands both co-dominated by *Picea glauca* and *Abies balsamea*. Its mean growth increment was 6.5 mm. Although the maximum growth rate was measured in stand no. 6 (7.2 mm), the difference in its growth rates between stands of different habitat types was not as great as it was for the preceding two feather mosses.

Cladina mitis showed a very small height growth increment of 0.8 mm in stand no. 1 of the *Picea glauca/Linnaea borealis* h.t. and a negative increment of -1.8 and -0.2 mm in stand nos. 2 and 8. This may indicate that *C. mitis* is still increasing in abundance (or at least holding its own) in stand no. 1, but declining in nos. 2 and 8. More replication of these measurements in each stand may be necessary to determine if these apparent trends are real.

Peltigera malacea had a measured height growth decrement of -0.4 mm in stand no. 2. Whether the crank wire method gives a fair measure of growth in *Peltigera* species is questionable in view of the lateral orientation of these thalloid lichens. The observed growth decrement may be more indicative of decomposition and settling of the substrate than it is of lichen growth.

The following mosses were measured in one stand only:

Brachythecium salebrosum, 11.8 mm in no. 5;
Plagiomnium cuspidatum, 3.6 mm in no. 5;
Tomenthypnum nitens, 9.4 mm in no. 7;
Aulacomnium palustre, 8.8 mm in no. 7;
Sphagnum angustifolium, 20.7 mm in no. 7;
Sphagnum warnstorfii, 19.2 mm in no. 7.

It may be noteworthy that the two peatmoss (*Sphagnum*) species grew twice as fast as the two brown moss (*Tomenthypnum* and *Aulacomnium*) species in stand no. 7 in 1983.

3.4.2 Growth during the 1983 Snow-free Season

Based on height measurements at five monthly intervals in 1983, the pattern of growth exhibited by the three feather mosses is very similar, namely a growth decrement during May, followed by the largest monthly increment in June, with progressively slower growth in July and August. However, there is some evidence that *Pleurozium schreberi* growth continues longer, into late summer and autumn, than do those of the other two feather mosses. The apparently negative height growth at the

start of the snow-free season is probably caused by substrate adjustments to decomposition, winter frost action, and spring rains.

Sphagnum angustifolium and *S. warnstorfii* grew most rapidly later in the season (July or August) than the feather mosses (June). The monthly growth rate of *S. warnstorfii* was much more stable than that of *S. angustifolium*.

Two other wetland mosses, *Tomenthypnum nitens* and *Aulacomnium palustre*, appear to have bimodal growth peaks in early and late summer, with a marked reduction in growth in July. Whether this growth pattern is typical of the two species is not known at present, but the next two years should give added insight.

It is noteworthy that none of the four above-mentioned wetland species showed the early season "negative growth" observed in the feather mosses.

The two poplar forest mosses studied, *Brachythecium salebrosum* and *Plagiomnium cuspidatum*, are not well suited to the cranked wire method of growth measurement since their growth is more horizontal than vertical. Nevertheless, both species exhibited the same early summer growth decrement observed in the feather mosses. *Brachythecium* appears to have a modest growth peak in June and a much larger one in August; July growth was only 0.6 mm. *Plagiomnium* grew fastest in June (8.6 mm), then fell off greatly to 0.6 mm in July and -0.8 mm

in August.

The lichens studied displayed no clear patterns of growth. In stand nos. 1 and 2 *Cladina mitis* showed peak growth in July; in stand no. 8 its peak was in May. *Peltigera malacea* had a positive growth increment only in June.

3.5 PHENOLOGY OF VASCULAR PLANTS

The phenological observations made in 1982 and 1983 were designed to monitor vascular plant populations through the entire sequence of events beginning with the swelling of vegetative and reproductive buds in the spring and continuing through leaf senescence and seedfall in autumn (Table 1). In order to describe and compare the phenologies of species, stands, and years, however, it is convenient to focus attention on the dates of achievement of biologically significant and definable developmental states along this chronosequence. The unfolding of new leaves and the opening of flower buds are relatively unambiguous events which signify that vegetative and reproductive processes are well underway. Hence, for each monitored population, the date when 50% of the individuals had reached these states was determined (in the case of flowering, 50% of the individuals which eventually flowered). Linear interpolation between sampling dates was applied. For each species, the dates for the monitored populations were combined into a stand mean, and stand means (for

those stands in which the species was observed) combined into an annual mean. Finally, the 1982 and 1983 means were combined to give an average date of leafing out and flowering for each species over the two snow-free periods.

3.5.1 Vegetative Phenology

Figure 3 shows the average date of leaf unfolding, as well as the range of observed stand means, for most species occurring in the reference stands. Species are arranged from earliest to latest within growth-forms.

Tree species separate into two discrete groups: early-expanding deciduous species, including broadleaf and needleleaf (i.e. *Larix laricina*) and later expanding, evergreen needleleaf species. Among the latter, *Pinus banksiana* and *Picea mariana* are particularly late in needle elongation, which sometimes does not occur until July.

Most species of deciduous shrubs produce leaves contemporaneously during a short period in late May. Conspicuous exceptions are several species of the genus *Salix* and *Alnus crispa*, which leaf out in early June. Like evergreen tree species, evergreen shrubs typically produce new leaves several weeks after their deciduous associates. *Linnaea borealis* is one evergreen species which commonly begins its vegetative growth early in the season.

FIGURE 3.
Vegetative phenological spectrum for vascular plant species in the Hondo - Lesser Slave Lake study area of north central Alberta. Based on 1982 and 1983 observations in the eight reference stands. Vertical line gives mean date when 50% of current year's leaves were fully expanded on monitored populations; horizontal line gives range of dates. Species arranged in chronological order within their growth-form group; POBA = Populus balsamifera, etc.

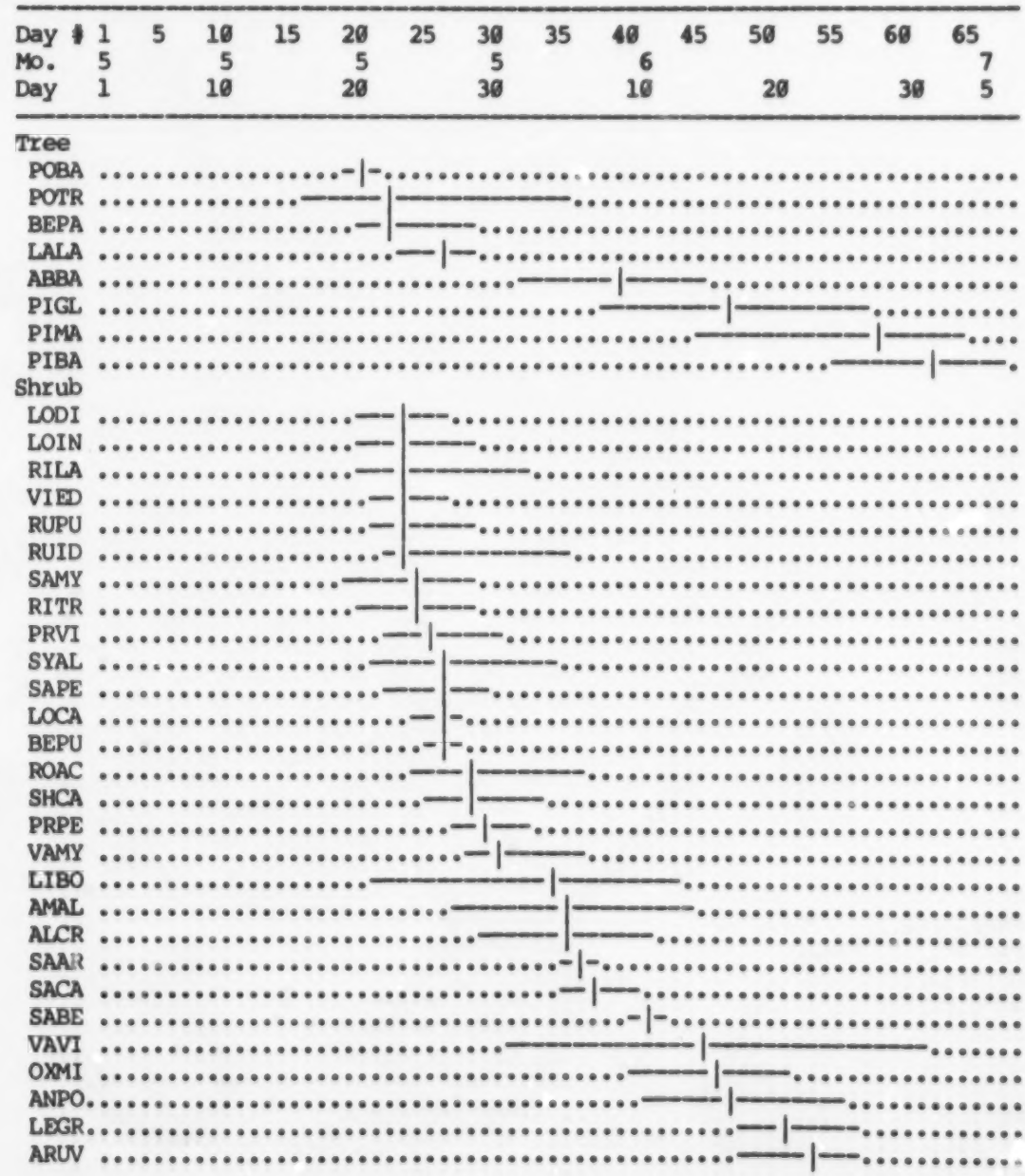


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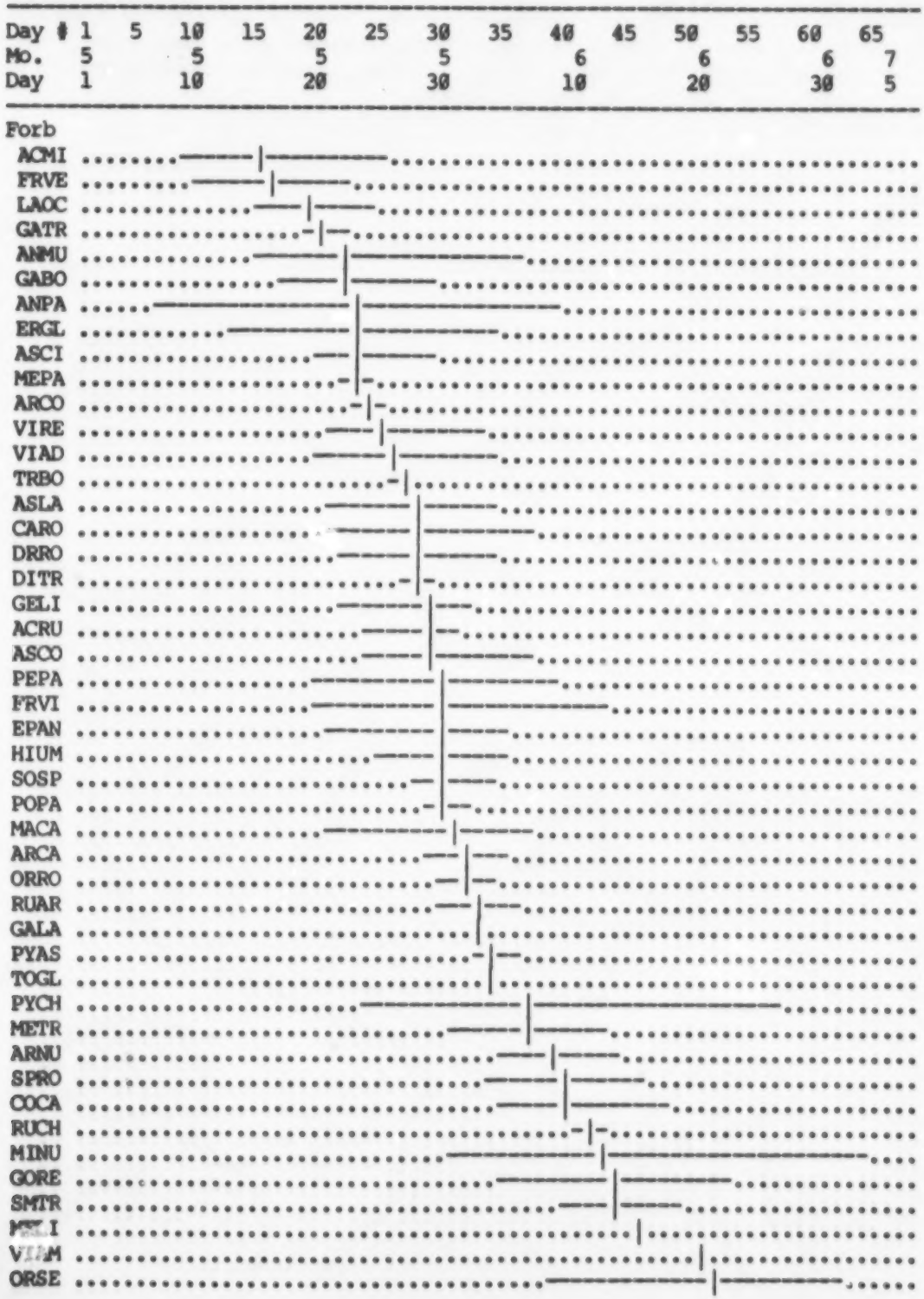
FIGURE 3. Continued



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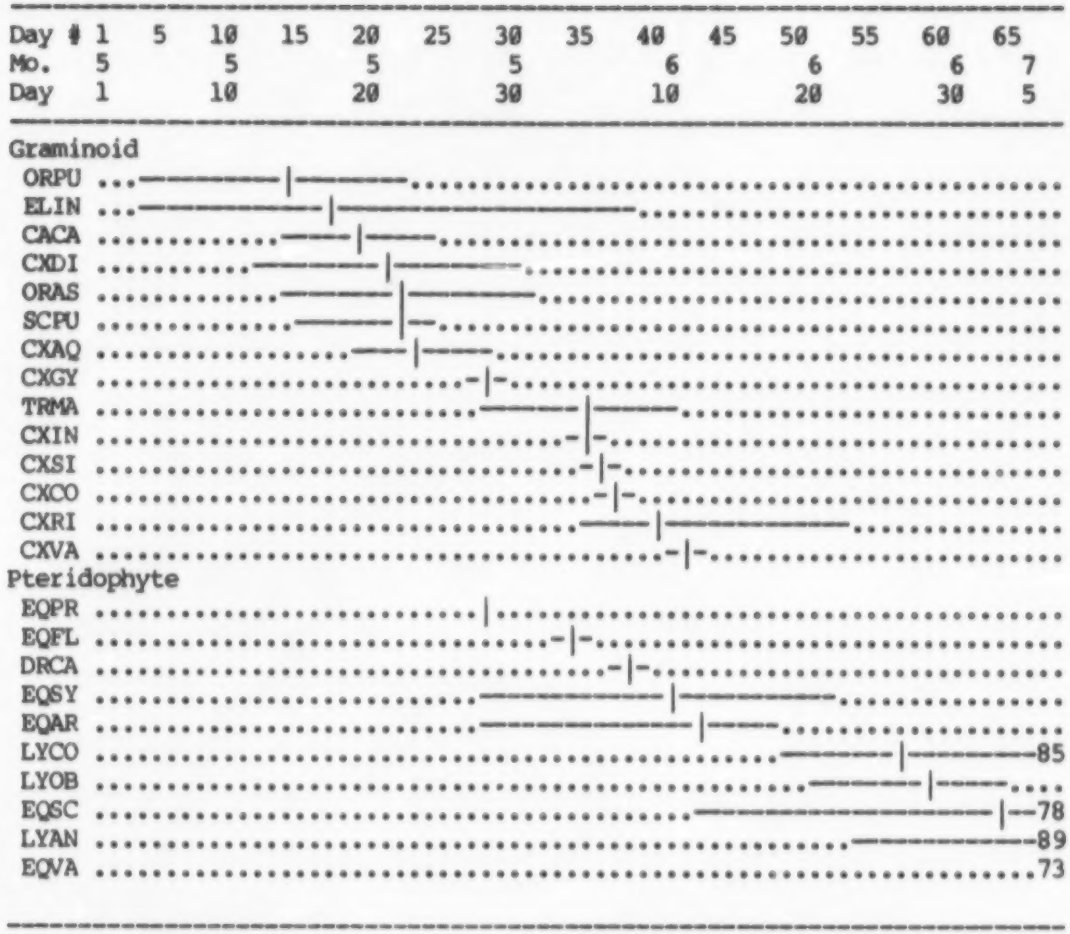

Although several forbs are quite early in initiating vegetative growth, the majority of species do not unfold their leaves until a few days after the deciduous shrubs have done so. Wintergreen forbs (*Cornus canadensis*, *Mitella nuda*, *Orthilia secunda*, etc.) generally produce new leaves later. Forbs restricted to peatland habitats are also later. *Melampyrum lineare*, one of two annual species in the reference stands, is one of the latest forbs in terms of vegetative phenology; it parasitizes the roots of other species.

Because most graminoids maintain leaves in mature and immature states throughout the summer, it is difficult to detect changes in their overall vegetative phenology. Nevertheless, our observations clearly show that many graminoid species are among the first to commence vegetative growth. Early- and late-developing groups are not restricted in terms of habitat, though most early species are characteristic of upland sites.

Pteridophytes, compared with the graminoids, have growth habits which fit even less neatly into the phenological categories used (Table 1), and are generally very slow to begin vegetative growth.

3.5.1.1 Annual Variations (1982 cf. 1983)

Comparisons of the rate of phenological development between years, in conjunction with the monitoring of environmental variables, might eventually suggest factors underlying the timing of vegetative and

reproductive events. Species which were monitored in both 1982 and 1983 in the same stand were divided into three groups: (1) those whose leaves unfolded earlier (by at least 5 days) in 1983; (2) those unfolding earlier in 1982; and (3) those leafing out within the same 4-day period in both years. The number of species in each group is listed by stand below.

Stand No.	Earlier in 1983	Earlier in 1982	Same in 1982 and 1983
1	15	3	6
2	12	1	8
3	6	6	12
4	6	5	9
5	2	10	13
6	10	7	16
7	4	11	10
8	6	5	8
Total	61	48	82

Sixty-one (32%) of the 191 species comparisons were earlier in 1983, while only 48 (25%) were earlier in 1982. Stand nos. 1 and 2, the two open pine stands, were advanced in terms of vegetative phenology in 1983 as compared with 1982. In contrast, plants in stand nos. 5 and 7 tended to leaf out earlier in 1982.

Correlation of phenological development with environmental measures such as soil temperature, soil moisture, air temperature, and light characteristics awaits further analysis. Snowpack characteristics and duration might also be of significance; snowpack studies were initiated in the winter of 1983-84 by Ross Hastings

(see section 2.9).

3.5.1.2 Variations Among Stands

Just as annual variation in the physical environment might be expected to influence the rate of plant development in a single stand, environmental heterogeneity among stands within the same year might similarly affect developmental processes. The matrices of inter-stand comparisons for dates of leafing out of "common" species in 1982 (Table 10) and 1983 (not shown) indicate that vegetative development began relatively early in both years in stand nos. 3, 5, and 6, while stand nos. 1, 2, 7, and 8 were slower in initiating growth. Plants in stand no. 5 were especially precocious in leafing out in 1982; of the 111 inter-stand comparisons involving populations in this aspen-dominated stand, 59 were 5 days or more earlier in it, while only 6 were later in it. Perhaps the most surprising result from Table 10 is the relatively slow vegetative development of plants in stand nos. 1 and 2, the young pine stands on sand. These stands are open and well-drained, with rapidly warming ground surfaces and air temperatures in the spring. Low nightly spring temperatures and the insulating effects of fruticose lichen carpets (e.g., Cladina mitis) may be contributing factors in delaying vegetative processes.

In this connection, it is important to emphasize that the inter-stand differences have been consistent in

Table 10. Comparisons of vegetative phenology of vascular plant species monitored within pairs of reference stands in the Hondo - Lesser Slave Lake study area in 1982. Numbers outside parentheses give number of species which leafed out[a] ≥ five days earlier in stand (row) than in stand compared with (column); numbers inside parentheses give number of monitored species common to both stands.[b]

Stand No.	Compared with Stand Number								
	1	2	3	4	5	6	7	8	Row Total
1	-	7(28)	0(24)	3(13)	0(12)	0(14)	.2(5)	3(10)	15(106)
2	8(28)	-	0(23)	0(15)	0(10)	1(12)	1(5)	2(9)	12(102)
3	15(24)	16(23)	-	6(20)	2(17)	1(19)	3(7)	6(12)	49(132)
4	7(13)	6(15)	3(20)	-	0(24)	4(25)	4(7)	9(14)	33(118)
5	8(12)	7(10)	6(17)	13(24)	-	12(35)	3(3)	10(10)	59(111)
6	10(14)	5(12)	4(19)	9(25)	4(35)	-	2(4)	7(9)	41(118)
7	1(5)	2(5)	3(7)	1(7)	0(3)	0(4)	-	3(17)	10 (48)
8	1(10)	2(9)	1(12)	2(14)	0(10)	0(9)	4(17)	-	10 (81)
Col. Tot.	50 (106)	45 (102)	17 (132)	34 (118)	6 (111)	18 (118)	19 (48)	40 (81)	

[a] ≥ 50% of new leaves were expanded (unfolded) on monitored populations.

[b] e.g., of the 20 species monitored in both stand nos. 3 and 4, 6 leafed out earlier in no. 3, three leafed out earlier in no. 4, and 11 leafed out at about the same time in both stands.

both years of the study, while annual fluctuations varied in direction depending on stand. Nevertheless, there is more consistency among stands within a year than vice versa. Of the 191 comparisons of species monitored in both years in the same stands, only 82 (43%) showed that leaf maturation occurred during the same 4-day period in 1982 and 1983. On the other hand, 72% of the 816 inter-stand comparisons in 1982, and 75% of the 326 comparisons in 1983, were synchronized in terms of vegetative phenology. While changes in observers between years certainly had some effect, it appears that vegetative phenology is primarily a function of macroclimatic elements which override stand environmental factors.

3.5.2 Reproductive Phenology

Figure 4 shows the spectrum of mean flowering dates (vertical marks) for plant species which flowered in 1982-1983 along with the range of stand means (horizontal lines). This spectrum vividly illustrates the wide range of flowering dates spanned by plants in boreal forest ecosystems.

Anemone patens flowers soon after snowmelt; flowering of other forb species is very evenly distributed over the 25 May - 15 August period, i.e. there is no single period in which the flowering of many species is concentrated. Graminoids too have a broad spectrum of flowering phenology, although they could be

FIGURE 4.

Reproductive phenological spectrum for vascular seed plant species in the Hondo - Lesser Slave Lake study area of north central Alberta. Based on 1982 and 1983 observations in the eight reference stands. Vertical line gives mean date when 50% of the flowers have reached maturity (anthesis) on monitored populations which flower; horizontal line gives range of flowering dates. Species arranged in chronological order within their growth-form group; BEPA = Betula papyrifera, etc.

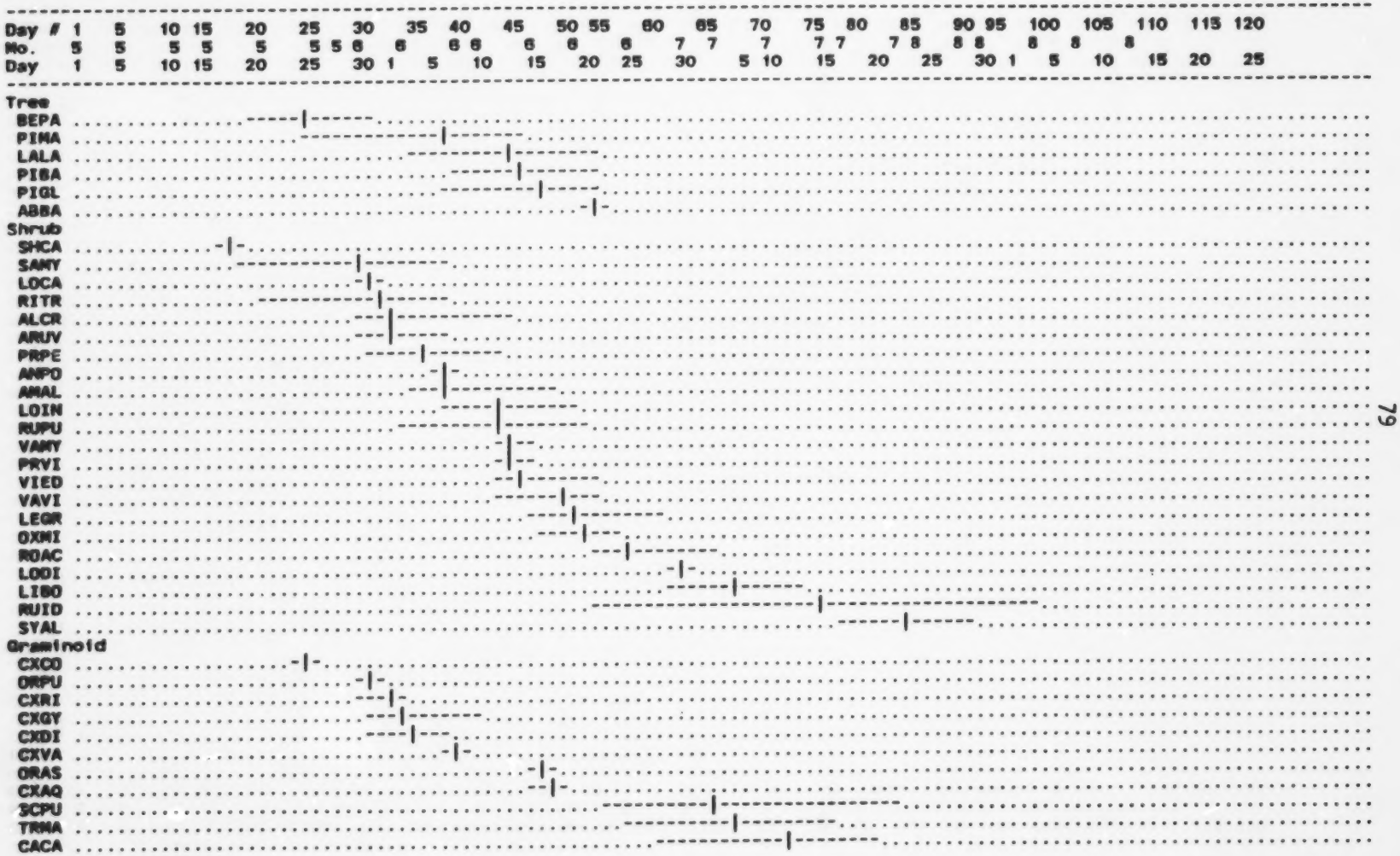

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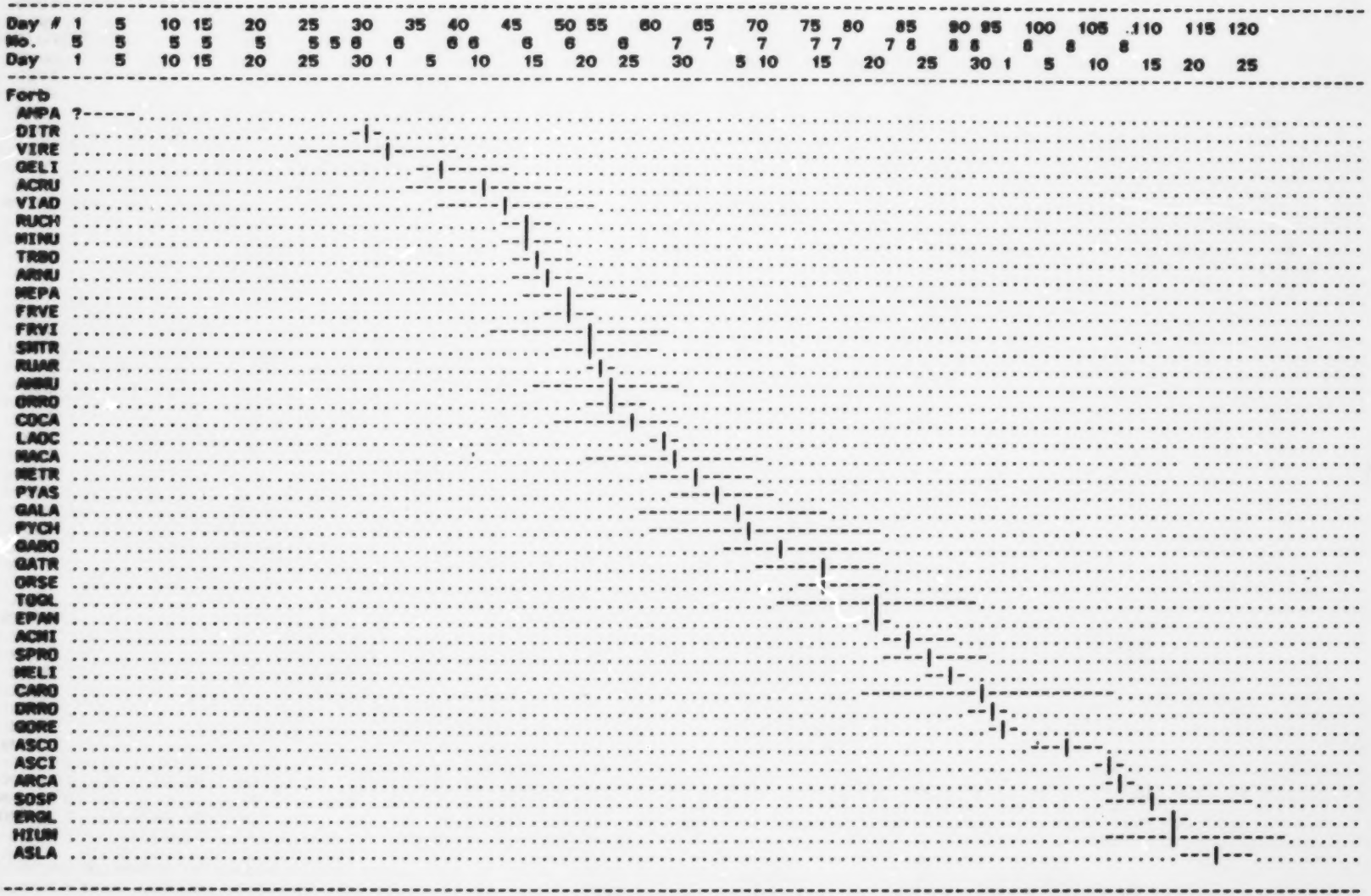
FIGURE 4. Concluded



divided into early- (mostly *Carex* species) and late-flowering groups. Shrubs, however, do have a modal period (25 May - 20 June) during which the flower buds of most species open. As a group, shrubs flower somewhat earlier than forbs. This strategy may be resource-related or associated with the location of receptors of light stimuli, presumably in the bud scales. Boreal tree species, which are all wind-pollinated, are nevertheless separated into two distinct phenological groups. Deciduous angiosperms such as *Betula papyrifera* (and *Populus* species, ch have not been observed to flower in the reference stands in 1982 or 1983) release their pollen in May, prior to the time that their leaves unfold. Coniferous species, including the deciduous *Larix laricina*, all shed their pollen during a brief period in mid-June.

Whereas the characteristic vegetative phenological sequence of species is associated with leaf persistence (evergreen and wintergreen plants leafing out relatively late) and habitat (peatland species leafing out late), the same patterns do not hold for reproductive phenology. Wintergreen forbs and evergreen shrubs include both early- and late-flowering types, as do peatland species. In fact, the latest-flowering plants in the study area are species of the family *Compositae* which are characteristic of the driest, early-successional pine stands.

3.5.2.1 Annual Variations (1982 cf. 1983)

The table below lists the number of species monitored in the same stand in both 1982 and 1983 which flowered 5 or more days earlier in one year than the other or which flowered during the same four-day period.

Stand No.	Earlier in 1983	Earlier in 1982	Same in 1982 and 1983
1	9	0	7
2	4	4	9
3	1	2	5
4	3	2	2
5	1	3	6
6	5	3	6
7	5	5	7
8	1	1	5
Total	29	22	47

Only in stand no. 1, where 9 of 16 species flowered earlier in 1983, was the effect of year convincing. Stand no. 1 was one of the two stands whose monitored populations leafed out earlier in 1983 (Section 3.5.1.1). Neither stand no. 2, which was also vegetatively earlier in 1982, nor stands nos. 5 and 7, where leaf unfolding was earlier in 1983, showed strong evidence of parallel trends in reproductive phenology.

3.5.2.2 Variations Among Stands

The matrices of inter-stand comparisons for date of flowering in 1982 (Table 11) and 1983 (not shown) do not show the consistent year-to-year ranking of stands that was reported for initiation of vegetative growth (section 3.5.1.2). Table 11 indicates that stand nos. 2,

Table 11. Comparisons of reproductive phenology of vascular plant species monitored within pairs of reference stands in the Hondo - Lesser Slave Lake study area in 1982. Numbers outside parentheses give number of species which flowered[a] ≥ 5 days earlier in stand (row) than in stand compared with (column); numbers inside parentheses give number of species for which at least one monitored population flowered in both stands.

Stand No.	Compared with Stand Number								
	1	2	3	4	5	6	7	8	Row Total
1	-	0(15)	0(7)	1(4)	0(3)	0(4)	0(0)	0(1)	1(34)
2	8(15)	-	2(13)	2(6)	0(4)	2(6)	0(2)	1(3)	15(59)
3	2(7)	1(13)	-	3(7)	0(6)	2(7)	1(3)	2(5)	11(48)
4	0(4)	0(6)	0(7)	-	0(10)	1(10)	0(4)	0(0)	1(41)
5	2(3)	2(4)	0(	4(10)	-	6(17)	0(1)	1(5)	15(46)
6	2(4)	2(6)	0(7)	2(10)	4(17)	-	0(1)	1(5)	11(50)
7	0(0)	0(2)	0(3)	2(4)	0(1)	1(1)	-	1(6)	4(17)
8	0(1)	0(3)	1(5)	0(0)	1(5)	1(5)	0(6)	-	3(25)
Col. Tot.	14 (34)	5 (49)	3 (48)	14 (41)	5 (46)	13 (50)	1 (17)	6 (25)	

[a] ≥ 50% of eventual flowering had occurred in monitored populations.

3, and 5 were advanced in terms of flowering in 1982 in comparison to the stands with which they shared common species. Stand no. 2 would have appeared much less precocious if it did not have so many species in common with stand no. 1, in which reproductive phenology was delayed in 1982 cf. 1983. In 1983 only stand no. 3 was definitely earlier in its reproductive phenology, with 9 early and 3 late comparisons among a total of 26. Thus stand no. 3, a mature pine forest on a southwest-facing slope (see Figure 12), was the only stand to support early reproductive and vegetative phenology in both years.

The consensus of the plant physiology literature indicates that initiation of vegetative growth is generally controlled by temperature, while flowering is usually controlled by photoperiod. However, species respond differently to both of these factors, and interactions with other factors can modify the primary response. Since photoperiod should be identical among stands and between years, one would expect fewer inter-stand and annual differences for flowering than for vegetative phenology. How well were these expectations met during 1982 and 1983 at Hondo? In fact, there were only slight differences in the percentage of inter-stand comparisons with more than 5 days' difference in 1982 (vegetative = 28%; reproductive = 20%) or 1983 (vegetative = 25%; reproductive = 17%), or in the

percentage of significant annual (between-year) comparisons (vegetative = 57%; reproductive = 53%). Clearly, other factors besides photoperiod are contributing to the timing of flower production.

3.6 ABOVE-GROUND SHOOT BIOMASS, LEAF AREA AND SHOOT COVER RELATIONSHIPS OF FORB SPECIES

As indicated in sections 3.5 and 4.7 of the First Report and section 3.6 of the Second Report, the three most important quantitative attributes of vascular plant populations and communities selected for estimation in this project are live shoot cover, live leaf area, and live shoot biomass. Whereas shoot cover is estimated directly at monthly intervals during the snow-free season in the reference stands, leaf area and shoot biomass are estimated indirectly using best-fit regression equations. In this section we (1) give such equations for 36 species of perennial forbs, i.e. broad-leaved herbaceous plants, and (2) show how the equations can be used to estimate and compare the leaf area and shoot biomass of these important understory species in the reference stands.

Three least squares equations were fitted: linear ($y = a + bx$); polynomial ($y = a + bx + cx^2 + dx^3 + ex^4$); and allometric ($y = ax^b$). The dependent variables are live shoot biomass (*SB*) and leaf area (*LA*); and the independent variables are live shoot cover (*SC*), shoot height (*SH*), and *LA*. Separate equations were computed for plants collected in 1981, 1982, and 1981+1982.

Of the 108 species attribute models sought for the 1982 data-set (i.e. 3 combinations of dependent and independent variables ([*SB/LA*; *SB/SC*; *LA/SC*] x 36 species), only 7 were not well fitted by a linear equation. Examination of the scatter diagrams of these 7 apparent exceptions revealed that most were unduly influenced by one or two "outliers" (i.e. points far removed from the regression line) and would otherwise be well fitted by a linear equation. The 1981 data-set was not as large or as systematically collected as the 1982 data-set, and contained more outliers also. Hence we conclude that linear regression equations adequately portray the relationships among *SC*, *SB*, and *LA* for the 36 species of boreal forbs.

A systematic comparison of the 1981 and 1982 equations for estimating *SB* from *LA* (see also Table 6 in Second Report) revealed that the slope coefficients (i.e. "*b*" values) of 10 of the 36 species were significantly higher ($P>0.95$) in 1982 than in 1981. This may indicate that the ratio of *SB*:*LA* was influenced by environmental differences between the two years. It may not be coincidental that many forb species also had higher mean shoot cover in 1982 cf. 1981. Despite these apparent annual variations in equation coefficients for *ca*. 30% of the forbs, equations based on pooled data-sets (1981+1982) give very acceptable estimates of both *SB* and *LA* for all forb species. Table 12 gives the equations

Table 12. Least squares regression equations for leaf area and shoot biomass of 36 forb species in the Hondo - Lesser Slave Lake area of north central Alberta. Based on data from pooled plant collections from 1981 and 1982.

Model 1.[a] LEAF AREA = a + b (SHOOT COVER)

Species	n	a	b	R^2	F
Achillea millefolium	60	5.81	0.110	0.03	2
Actaea rubra	36	21.91	0.853	0.71	83
Anemone multifida	48	9.11	0.890	0.46	39
Anemone patens	26	2.27	0.756	0.42	17
Aralia nudicaulis	125	29.94	0.938	0.80	505
Aster ciliolatus	61	3.52	1.036	0.86	351
Aster conspicuus	32	21.87	1.624	0.78	109
Aster laevis	55	5.52	1.032	0.66	103
Campanula rotundifolia	80	4.55	0.803	0.41	55
Cornus canadensis	137	4.55	0.718	0.67	274
Drosera rotundifolia	13	0.76	0.115	0.08	1
Epilobium angustifolium	69	-8.92	2.110	0.76	210
Erigeron glabellus	44	-2.05	1.336	0.74	117
Fragaria virginiana	101	0.07	1.016	0.81	428
Galium boreale	168	1.67	1.295	0.45	138
Galium triflorum	32	4.23	0.662	0.83	148
Geocaulon lividum	119	4.76	1.481	0.64	210
Goodyera repens	29	-0.48	1.094	0.54	32
Hieracium umbellatum	31	-5.78	1.793	0.62	47
Lathyrus ochroleucus	40	-3.54	1.464	0.83	186
Maianthemum canadense	172	4.37	0.779	0.71	416
Mertensia paniculata	77	11.32	1.170	0.61	120
Menyanthes trifoliata	21	0.26	1.087	0.80	76
Mitella nuda	114	0.33	0.912	0.82	497
Orthilia secunda	97	2.99	0.832	0.59	134
Petasites palmatus	98	-0.45	0.950	0.88	731
Petasites sagittatus	17	4.93	0.923	0.86	90
Pyrola asarifolia	51	2.67	1.041	0.57	64
Pyrola chlorantha	67	-0.15	1.189	0.61	102
Rubus arcticus	11	9.20	0.320	0.18	2
Rubus chamaemorus	23	-0.27	1.101	0.91	207
Smilacina trifolia	44	6.45	0.883	0.86	263
Solidago spathulata	52	1.35	1.105	0.63	85
Trientalis borealis	50	2.45	0.833	0.77	157
Viola adunca	30	-5.19	1.683	0.92	325
Viola renifolia	71	1.07	0.965	0.87	484

[a] Leaf area and shoot cover in sq cm; shoot biomass in grams

continued ...

Table 12. continued

Model 2.[a] SHOOT BIOMASS = a + b(SHOOT COVER)

Species	n	a	b	R^2	F
Achillea millefolium	60	0.0293	0.00379	0.50	57
Actaea rubra	36	0.0777	0.00453	0.66	67
Anemone multifida	48	0.0980	0.0166	0.44	36
Anemone patens	26	0.3630	0.00366	0.05	1
Aralia nudicaulis	125	0.1957	0.00531	0.75	366
Aster ciliolatus	60	-0.0512	0.00859	0.71	141
Aster conspicuus	31	0.1580	0.0111	0.54	35
Aster laevis	55	-0.0621	0.0209	0.57	70
Campanula rotundifolia	79	0.0606	0.0128	0.36	43
Cornus canadensis	136	0.0221	0.00481	0.58	182
Drosera rotundifolia	13	0.0086	0.00220	0.49	10
Epilobium angustifolium	68	-0.0431	0.0151	0.78	231
Erigeron glabellus	43	-0.0347	0.0200	0.59	59
Fragaria virginiana	100	0.0303	0.00778	0.72	257
Galium boreale	167	0.0187	0.00769	0.51	169
Galium triflorum	32	0.0202	0.00319	0.62	48
Geocaulon lividum	119	0.0584	0.0108	0.47	103
Goodyera repens	28	0.0073	0.0133	0.39	16
Hieracium umbellatum	30	-0.0281	0.0183	0.64	49
Lathyrus ochroleucus	39	-0.0373	0.00828	0.83	177
Maianthemum canadense	170	0.0345	0.00486	0.41	115
Mertensia paniculata	77	0.1093	0.00723	0.51	77
Menyanthes trifoliata	20	0.0274	0.0111	0.66	36
Mitella nuda	115	0.0053	0.00531	0.56	142
Orthilia secunda	97	0.0016	0.0137	0.67	195
Petasites palmatus	94	-0.0072	0.00449	0.87	591
Petasites sagittatus	17	0.0356	0.00476	0.61	24
Pyrola asarifolia	51	0.0356	0.0128	0.22	14
Pyrola chlorantha	67	-0.0279	0.0198	0.61	100
Rubus arcticus	11	-0.0914	0.0125	0.76	28
Rubus chamaemorus	23	-0.0117	0.00814	0.89	163
Smilacina trifolia	44	0.0719	0.00312	0.55	51
Solidago spathulata	51	-0.0604	0.0263	0.46	41
Trientalis borealis	50	0.0110	0.00289	0.63	83
Viola adunca	30	-0.0557	0.0178	0.87	185
Viola renifolia	73	0.0032	0.00414	0.73	191

[a] Leaf area and shoot cover in sq cm; shoot biomass in grams.

continued ...

Table 12. Concluded

Model 3.[a] SHOOT BIOMASS = a + b (LEAF AREA)

Species	n	a	b	R^2	F
Achillea millefolium	80	-0.00398	0.0117	0.49	75
Actaea rubra	41	-0.00156	0.00496	0.87	258
Anemone multifida	52	0.0531	0.0137	0.54	59
Anemone patens	35	0.366	0.00234	0.03	1
Aralia nudicaulis	131	0.113	0.00525	0.79	492
Aster ciliolatus	84	-0.0236	0.00695	0.67	168
Aster conspicuus	34	-0.171	0.00760	0.86	196
Aster laevis	67	-0.0148	0.0153	0.55	81
Campanula rotundifolia	81	0.0465	0.0107	0.40	52
Cornus canadensis	170	0.00539	0.00648	0.66	325
Drosera rotundifolia	13	0.0113	0.00365	0.23	3
Epilobium angustifolium	73	0.0993	0.00644	0.84	379
Erigeron glabellus	48	0.0208	0.0135	0.67	92
Fragaria virginiana	134	0.0443	0.00701	0.74	366
Galium boreale	206	0.0295	0.00409	0.54	243
Galium triflorum	40	0.00344	0.00460	0.78	137
Geocaulon lividum	140	0.0270	0.00722	0.78	496
Goodyera repens	44	0.0134	0.0117	0.60	62
Hieracium umbellatum	32	0.155	0.00703	0.54	36
Lathyrus ochroleucus	57	0.0144	0.00485	0.78	191
Maianthemum canadense	209	0.0154	0.00558	0.50	208
Mertensia paniculata	98	0.0485	0.00606	0.83	462
Menyanthes trifoliata	22	0.0431	0.00875	0.73	55
Mitella nuda	158	0.00116	0.00611	0.70	364
Orthilia secunda	164	-0.0133	0.0135	0.74	471
Petasites palmatus	108	0.00320	0.00444	0.89	894
Petasites sagittatus	17	0.0256	0.00479	0.62	24
Pyrola asarifolia	134	-0.0184	0.0141	0.77	451
Pyrola chlorantha	105	-0.00716	0.0154	0.77	350
Rubus arcticus	11	-0.0177	0.00947	0.25	3
Rubus chamaemorus	23	0.0107	0.00707	0.89	171
Smilacina trifolia	57	0.0488	0.00365	0.70	131
Solidago spathulata	71	-0.00377	0.0182	0.50	68
Trientalis borealis	78	0.00354	0.00343	0.89	634
Viola adunca	45	-0.00023	0.0105	0.96	1087
Viola renifolia	126	0.00686	0.00381	0.79	469

[a] Leaf area and shoot cover in sq cm; shoot biomass in grams.

for *SB* and *LA* based on the pooled data-sets.

Using the equations in Table 12 we have computed estimates of shoot biomass and leaf area for 16 forb species populations in stand no. 3 from the 3 August 1983 shoot cover data (Table 5) with species listed in order of decreasing estimated shoot cover (Table 13).

Aralia nudicaulis was the dominant forb with an estimated shoot cover of 1,008 sq m/ha, shoot biomass of 53.52 kg/ha (oven-dry matter @ 65°C), and leaf area of 945.5 sq m/ha. Note that shoot cover exceeds leaf area because petioles and other non-leaf blade parts are included in the shoot cover estimate. *Maianthemum canadense* was the second-ranked forb, followed by *Cornus canadensis*, *Epilobium angustifolium*, *Orthilia secunda*, *Viola renifolia*, *Galium boreale*, and *Fragaria virginiana*, based on all three quantitative criteria. Thereafter the rank-ordering of species varies according to criterion (e.g., *Anemone patens* ranks no. 9 in terms of shoot cover but no. 11 in biomass and leaf area).

It is obvious from these data that forb species contribute considerable cover, biomass and leaf area to the understory of stand no. 3 in August, and that *Aralia nudicaulis*, in particular, must add significantly to the total primary production of the community.

Before this phase of the SEADYN project is completed, equations for other growth-forms will be computed and used.

Table 13. Estimated shoot cover, leaf area, and shoot biomass of 15 forb species in reference stand no. 3 on 3 August 1983. Based on ocular estimates of shoot cover in 25 5 x 5 m plots (Table 5) and regression equations (Table 12). Species listed in order of decreasing shoot cover.

Forb Species	Shoot Cover		Shoot Biomass		Leaf Area	
	%	sq m/ha	kg/ha	(rk)	sq m/ha	(rk)
Aralia nudicaulis	10.08	1,008.0	53.52	(1)	945.5	(1)
Maianthemum canadense	2.68	268.0	13.02	(2)	208.0	(2)
Cornus canadensis	1.26	126.0	6.06	(3)	90.5	(3)
Epilobium angustifolium	0.364	36.4	5.50	(4)	76.8	(4)
Orthilia secunda	0.328	32.8	4.49	(5)	27.3	(5)
Viola renifolia	0.216	21.6	0.89	(6)	20.8	(6)
Galium boreale	0.068	6.8	0.52	(7)	8.8	(7)
Fragaria virginiana	0.060	6.0	0.47	(8)	6.1	(8)
Anemone patens	0.020	2.0	0.073	(11)	1.5	(11)
Pyrola chlorantha	0.016	1.6	0.32	(9)	1.9	(10)
Hieracium umbellatum	0.012	1.2	0.22	(10)	2.2	(9)
Geocaulon lividum	0.005	0.5	0.054	(13)	0.7	(12)
Campanula rotundifolia	0.005	0.5	0.064	(12)	0.4	(13)
Anemone multifida	0.0008	0.08	0.013	(14)	0.1	(14.5)
Trientalis borealis	0.0008	0.08	0.002	(15)	0.1	(14.5)

3.7 POPULATION STRUCTURE OF TREE SPECIES

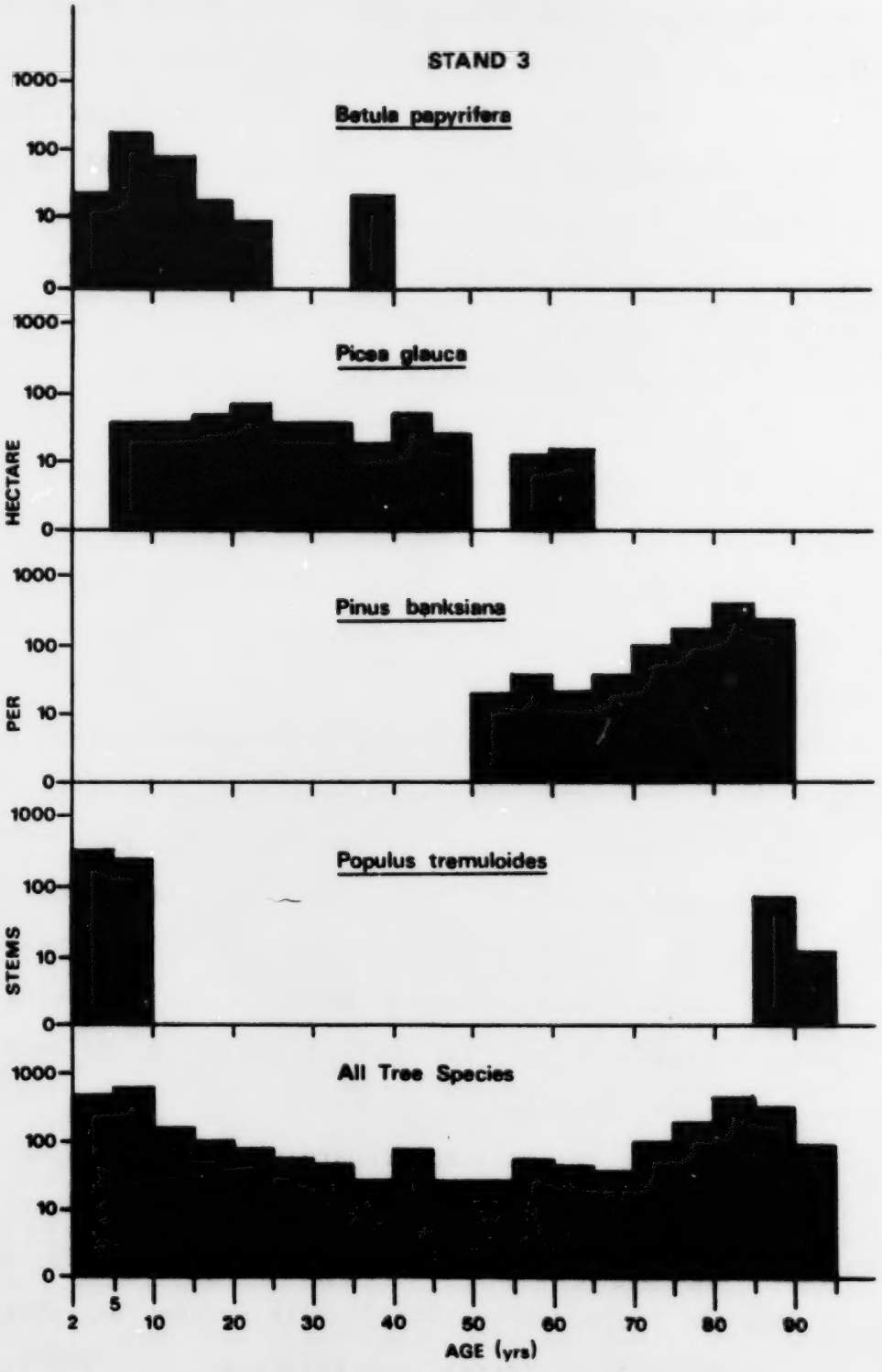
The age structure of a plant population is the historical result of births and deaths since its establishment. Age is relatively easy to determine for woody plants in temperate and boreal regions; annual rings leave an annotated record which registers not only the passage of time, but the growth conditions during each year. Juxtaposing the age structures and growth curves of all tree species within a community, one can begin to reconstruct the history of a forest through the rise and fall of its dominant species. The precise location of living trees of known age, as well as the identity and approximate date of death of decaying individuals can further elucidate stand history. We believe that such a case study approach, integrating these four sources of information, is a necessary first step in understanding successional processes in boreal forests. Extensive surveys of population age structure throughout a wider study area can then be used to test the successional models suggested from the intensive case studies.

In this section, tree population age structures are presented for three stands - nos. 3, 5, and 8. Stand no. 8, in particular, indicates how growth rates and spatial information can aid in reconstructing the histories of forests.

3.7.1 Age Structure in Reference Stand No. 3

Four distinctly different strategies are represented by the age structures in stand no. 3 (Figure 5). The strategy of *Pinus banksiana* is that of an opportunistic species able to reproduce and attain dominance for a fairly extended period after major disturbance, but unable to continue recruitment without further perturbation. Successful recruitment of *Populus tremuloides* stems to canopy position is restricted to a briefer period after disturbance, but a subpopulation of small aspen suckers is maintained in the understory of the undisturbed forest. Although mature aspen occurs almost exclusively in the upper northeast corner (see Figure 12), aspen suckers are distributed fairly uniformly throughout the stand. The spatial pattern of *P. tremuloides* is probably typical of clonal species, which can expand laterally by vegetative means into territory occupied by other species. *Betula papyrifera*, which reproduces exclusively from seed in stand no. 3, exhibits a population structure which could be produced by a constant rate of seedling recruitment (except in the last five years) with a fixed mortality rate under a closed forest canopy. The lack of older birch individuals may result from a combination of the following factors: seed source limitations, high mortality rate, and lack of appropriate seedbeds; all birch seedlings and saplings inspected have recruited on

Figure 5. Age structure of tree species populations in reference stand no. 3 in 1983. Based on tree ring counts from increment cores and internode counts from small specimens. See also Methods section 2.4.


STAND 3
Betula papyrifera
Picea glauca
Pinus banksiana
Populus tremuloides
All Tree Species
1000
100
10
0
HECTARE
PER
STEMS
2
5
10
20
30
40
50
60
70
80
90
AGE (yrs)

decaying logs. Like *Betula papyrifera*, *Picea glauca* did not recruit successfully until some years after the initiation of the current stand. Spruce differs from birch primarily in the under-representation of young individuals in the seedling and small sapling sizes. It appears that conditions three or four decades ago in stand no. 3 were more favorable for the establishment and survival of white spruce than they are at present.

Stand no. 3 was initiated approximately 85 years ago after a large-scale disturbance which left no surviving trees. Ring widths from cores of trees more than 100 years old in stand nos. 4 and 6 indicate that the 1898-1907 period was one of extremely slow growth. A series of dry years could have created conditions for extensive fire and/or an insect or disease epidemic. To date, no fire-scarred survivors have been located in the vicinity. Whatever the destructive agent, many of the trees which died *circa* 1899 appear to have remained standing for 35-40 years (see section 3.8). The logs derived from these standing dead trees eventually provided the seedbed for much of the birch and some of the spruce regeneration in the stand.

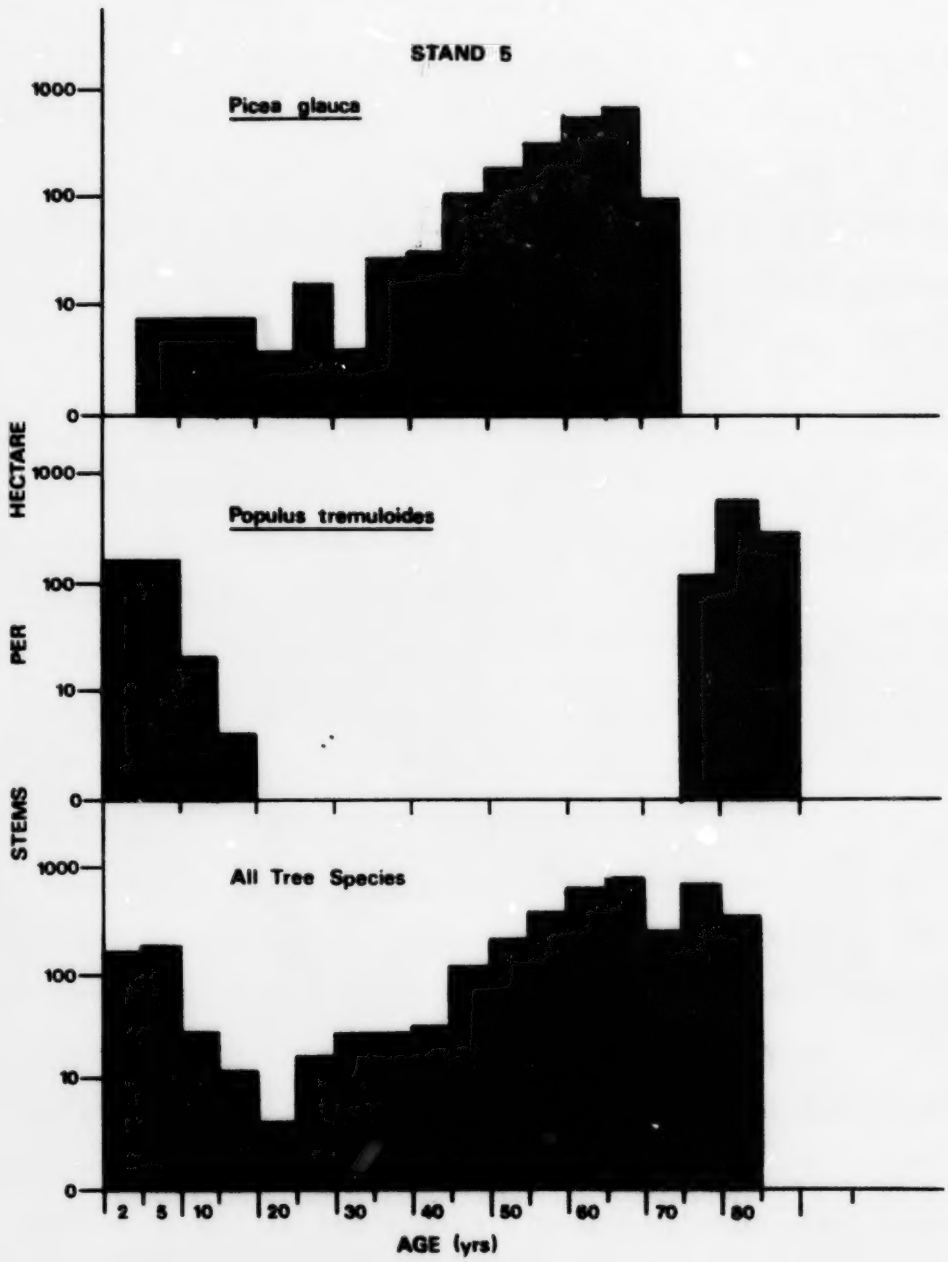
A critical question regarding succession (or the lack of it: Rowe 1979, Johnson 1979) in boreal forests is whether the "early successional" pine or aspen actually predate the "late successional" white spruce, or whether they simply grow faster (see Parminter 1983, who found

that white spruce is nearly always contemporary with aspen after fire in Northern British Columbia). Furthermore, if there is a delay in white spruce establishment, is it caused by intense post-disturbance competitive exclusion, by an inadequate seed source, or by the necessity for some preconditioning of the site associated with the presence of pine or aspen? In stand no. 3, which has a dense pine overstory, the oldest spruce germinated about 25 years after the initial wave of pine establishment. The two younger reference stands on sand (stand nos. 1 and 2) are more open 40- and 65-year-old *Pinus banksiana* stands with essentially no spruce representation to date. Although lack of an adequate seed source may be a contributing factor in some cases, it appears that *Picea glauca* has difficulty becoming established in the immediate post-fire environment on this habitat type. Once canopy closure has occurred, however, white spruce recruits and grows rapidly, and eventually replaces jack pine.

3.7.2 Age Structure in Reference Stand No. 5

The bimodal age structure of *Populus tremuloides* in stand no. 5 (Figure 6) is identical to that in stand no. 3. The age structure of *Picea glauca*, however, is skewed strongly to the left in stand no. 5, indicating a more successful entry of spruce into the aspen than the pine stand. There is also a shorter hiatus, about 15 years, between stand initiation and the first pulse of

Figure 6. Age structure of tree species populations in reference stand no. 5 in 1983. Based on tree ring counts from increment cores and internode counts from small specimens. See also Methods section 2.4.


STAND 5
Picea glauca
Populus tremuloides
All Tree Species
STEMS PER HECTARE
1000
100
10
0
2
5
10
20
30
40
50
60
70
80
AGE (yrs)

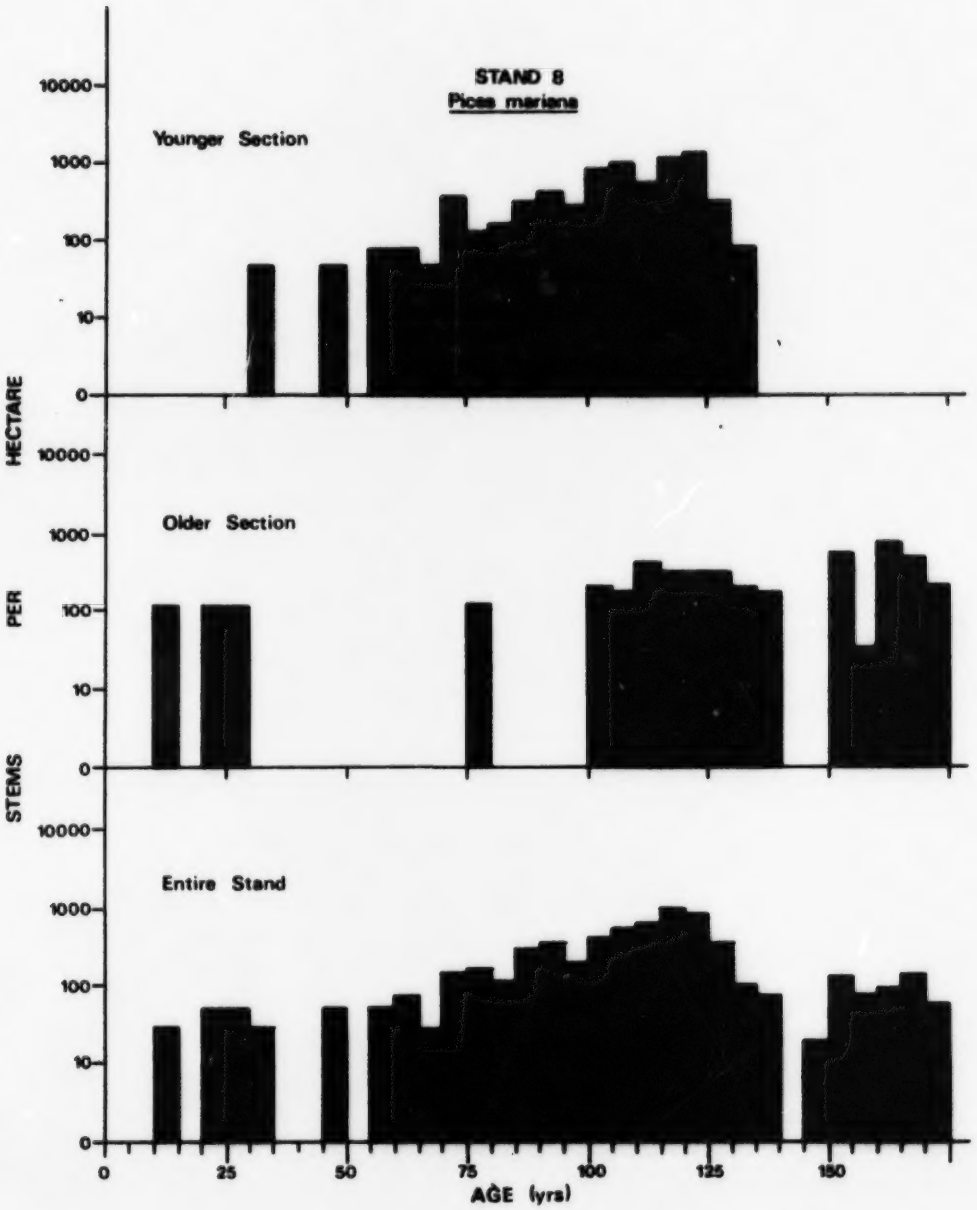
white spruce regeneration into stand no. 5. Again there is little current recruitment of spruce.

Stand no. 5 was initiated in about 1905, towards the end of the 1898-1907 decade of slow diameter growth. In Stand no. 6, less than 100 m away, *Populus tremuloides* growth was reduced much more during this period than that of *Picea glauca*. Still, it is very likely that stand no. 5 originated after fire; burn-scarred trees have been found between it and stand no. 6.

3.7.3 Age Structure in Reference Stand No. 8

The age distribution of *Picea mariana*, the only tree species with significant density in stand no. 8, is shown in Figure 7. The dominant trees in the stand occur in two age groups: 150-175 and 100-130 years. These two age groups are spatially separated within the 20 x 20 m central sector in which the ages of the larger trees were determined; a thin isthmus of older trees is embedded in a matrix of younger individuals of similar appearance and stature (Figure 8). The age structures of the *Picea mariana* subpopulation in the 4 plots with maximum tree age >150 years and in the 12 plots with maximum age <150 years are presented separately in the upper graphs in Figure 7. In the older part of the stand there was a relatively brief surge of recruitment at the same time as the initial wave in the younger part. Black spruce recruitment continued in the latter area for 60-70 years, but has been of little consequence in either part for the

Figure 7. Age structure of tree species populations in reference stand no. 8 in 1983. Based on tree ring counts from increment cores and internode counts from small specimens. See also Methods section 2.4.


STAND 8
Picea mariana
Younger Section
Older Section
Entire Stand
STEMS PER HECTARE
10000
1000
100
10
0
0
25
50
75
100
125
150
AGE (yrs)

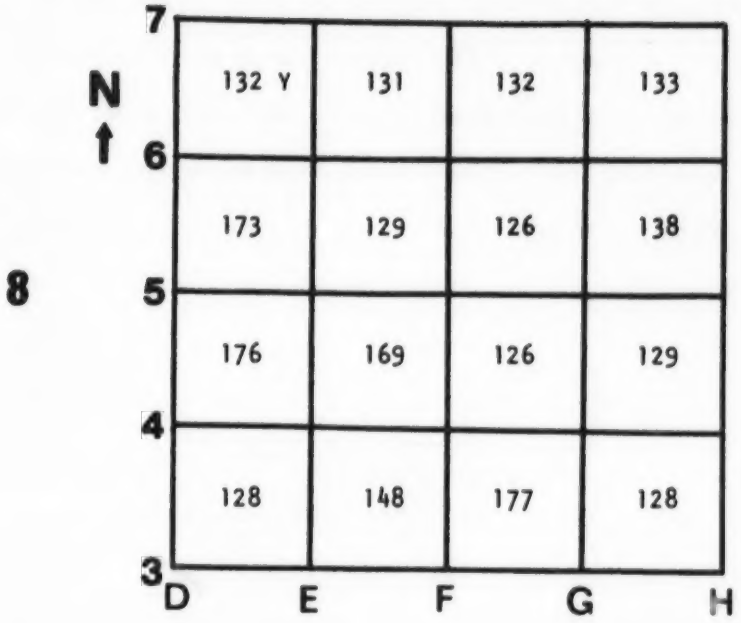


Figure 8. Maximum age of black spruce trees in the centrally located 16 5x5 m plots of reference stand no.8 in 1983. See also dimensions and orientation of reference stand in Figure 3 of the First Report.

last 50 years.

At least two scenarios could have produced the demographic and spatial patterns described above:

1. About 175 years ago an "island" of black spruce became established, presumably in some favorable, raised habitat in the fens surrounding nearby Bullet Lake. Forty years later the trees reached sexual maturity and began to disperse seeds into the surrounding area, which was not, until then, sufficiently drained to permit the development of a very dense black spruce stand.

2. A major perturbation (probably fire) created conditions favorable for development of an extensive *Picea mariana* forest in the year 1809. Around 1850 a second fire occurred, but left unburned patches of the 1809-initiated stand. The burned areas were rapidly re-occupied, and some regeneration also occurred under the surviving patches of black spruce.

The diameter growth curves for nine black spruce trees >150 years old (Figure 9) appear to support the second scenario. An abrupt increase in diameter growth occurred soon after the date of the proposed second fire. Such a release in growth might be expected if competition from neighbors was suddenly removed. Although the first scenario is not ruled out, a falling water table would probably stimulate a more gradual growth increment, and the effects of water level on establishment might not

Figure 9. Average radial growth of nine black spruce trees in reference stand no.8 during the period 1832-1882. Growth is expressed in mm per five 10-year intervals.

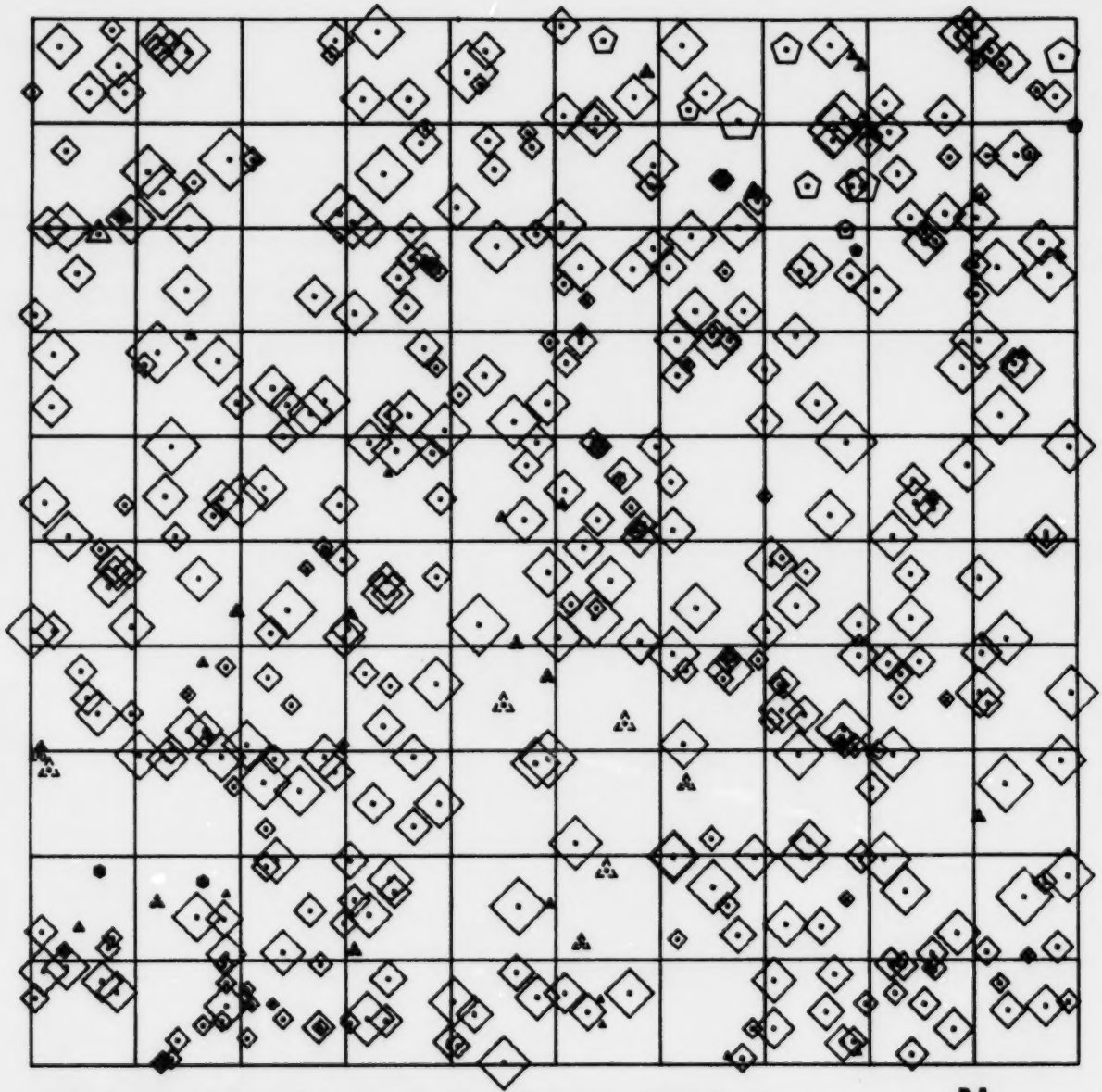
necessarily coincide with those on growth of mature trees.

3.7.4 Tree Dispersion on Stem Maps

A program for plotting tree locations has been written by Bill Lee, computer programmer-analyst for the SEADYN Project. Figure 10 is a reduced copy of the stem map generated by this program for stand no. 3. Species are represented by different polygons, which can also be color-coded. The sizes of the polygons in Figure 10 are proportional to stem diameter; however, polygon size can also be a function of age, height, crown width, or any other of the measured tree parameters. The stem map shows quite effectively (1) the apparently random dispersion pattern of *Pinus banksiana* trees (with the larger trees perhaps tending to occur more frequently than expected by chance in low-density areas?), (2) that *Picea glauca* generally occupies small gaps in the pine canopy, (3) the restriction of *Populus tremuloides* to the northeast corner of the stand, etc. The stem locations themselves can be used to determine indices of spatial dispersion, neighbor effects on radial increment, etc.

As tree growth and mortality occur in the reference stands and these data are tallied at annual intervals, the stem maps will be revised to show dynamic changes in the dispersion of tree parameters.

Figure 10. Stem map showing locations and diameters of living trees >2.5 cm DBH by species in reference stand no. 3 in 1981. There are 410 Pinus banksiana stems (◇), 80 Picea glauca (△), 21 Populus tremuloides (○), 2 Betula papyrifera (◎), and 2 Picea mariana (△). Symbols vary in size with tree DBH. See Methods section 3.6 in First Report.



Hondo-Slave Lake Tree Species Stem Map: Reference Stand No. 3
All Stems Mapped, with DBH Values in 2.0-cm Classes

N

3.8 DEAD AND DOWN TREES

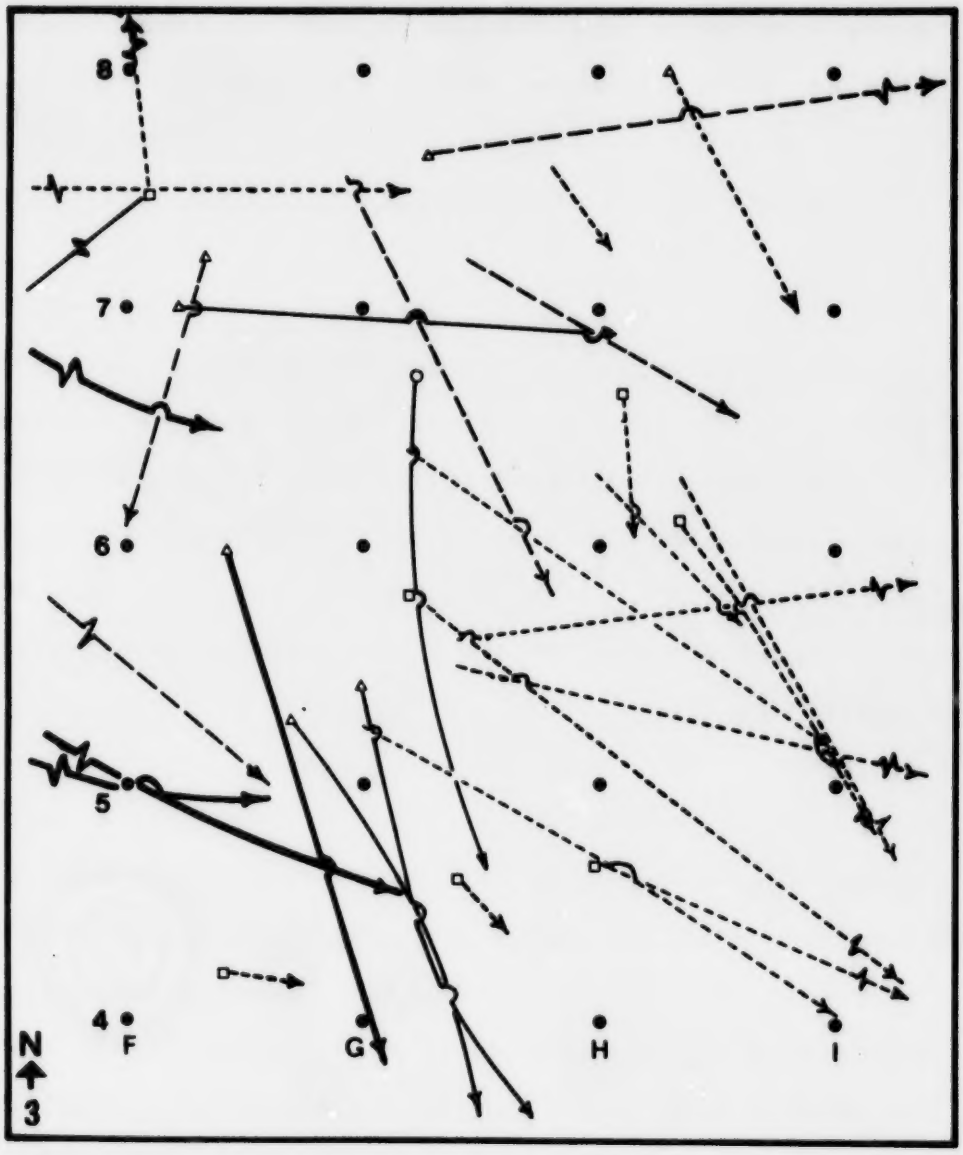
Summarization of the dead and down tree information from the eight reference stands is preliminary and primarily descriptive at present. Figure 11 maps the distribution of the dead and down tree component of a representative 15 x 20 m section of stand no. 3. All positively identified logs in this section, and all but one in the stand as a whole, are *Pinus banksiana*. Although no Decay Class 4 logs (hereafter abbreviated, e.g., DC4; see section 2.4.3) are present in the area pictured in Figure 11, all decay classes are represented somewhere in the stand. Dated tree falls outside the stand (section 2.4.3) suggest that a pine tree remains in each decay class for roughly 10 years once it falls; i.e., DC1 trees have been on the ground for up to 10 years, DC2 trees 11-20 years, etc. Pines which have been on the ground more than 50 years under these conditions are not identifiable or mappable without severe site perturbation.

Several patterns evident in Figure 11 appear to have general application throughout stand no. 3:

1. The direction of fall for a large majority of trees is towards the east, particularly the southeast. Storm fronts and the strongest winds in the Hondo area are generally from the northwest; these northwest winds are apparently directly or indirectly responsible for most tree falls.

Figure 11. Map of dead and down trees in the centrally located 12 5x5 m plots of reference stand no. 3 in 1983. Log "age" is the estimated number of years the tree has been on the ground. Log age-classes for this stand are:

These symbols indicate whether the trunk was broken off well above the base (O), broken at the base (△), uprooted (□), or too decayed to determine ( ). Where two logs intersect the (⌒) symbol indicates which log is on top.


8
7
6
5
4
F
G
H
I
N
3

2. Down trees of the same decay class are often found in clumps oriented in the same direction. The implication is that trees are often windthrown in groups. Hence a definite date for the fall of one tree could be applied to all trees within its group. However, it cannot be inferred that all individuals in the group died simultaneously, as some or all could have died prior to blowdown.

3. Pines in DC5 were uprooted when they fell, whereas trees falling more recently broke off at the base or higher up the tree trunk. Evidently the DC5 trees, which we estimate to have fallen about 50 years ago, had been dead since the time of the disturbance which led to initiation of the current stand. By the time the trees were uprooted, most of their root systems had apparently decayed, as there is little visible evidence of soil disturbance near the base of these logs. Live or recently dead trees which are uprooted often produce large mounds of soil which produce a characteristic hummock-and-hollow microtopography which may persist for hundreds of years. Perhaps, under the climatic conditions of this portion of the boreal forest, where extremely high wind speeds rarely occur, uprooting of live trees is restricted to very large and/or isolated individuals.

What are the implications of the observations on down trees in stand no. 3 with regard to stand history?

We postulate that the disturbance which led to the current forest destroyed a stand similar in composition, and possibly age, to the present one. Although other species present in the ancestral stand may have decayed more rapidly (e.g., *Populus tremuloides*), the number of DC5 pine logs identified indicates that *Pinus banksiana* was the dominant component. The size of the trees in the original forest is not easy to establish with great precision because of the extent of decay. However, the trees seem to have been no larger than those present today, i.e. 10-25 cm DBH.

Furthermore, the DC5 logs display evidence of the agent of destruction of the previous forest. Most of these down trees are charred several meters above their bases, down to and including the roots. It seems unlikely that the fire which scorched these trees occurred while they were standing dead among the developing pines, since no fire scars have been observed on currently living trees within the stand. The fire must have been very intense to have charred the roots of these trees. Another possibility is that the dead and down DC5 trees were killed by fire, were subsequently windfelled after their roots rotted, and then charred again by fire while on the ground. This latter hypothesis will be tested during the 1984 field season.

3.9 TOPOGRAPHY OF THE REFERENCE STANDS

The elevations determined with the Debenham levelling device at the 121 corner posts in the 50 x 50 m reference stands were converted into contour maps by the SURFACE II program (Sampson 1978) using a subroutine written by Bill Lee. The map for stand no. 3 (Figure 12) is an example of the output of the program. The general topographies of the eight stands are as follows:

No. 1 has a 5-10% slope from all directions towards a central hollow; no. 2 is essentially flat in its western 2/3, with a 3-10% east-facing slope in its eastern 1/3; no. 3 has a 6% slope towards the southwest, with a hollow near the southwestern corner; no. 4 has an irregular 3% slope towards the north; no. 5 has a 4% northeast-facing slope; no. 6 has a 2% north-facing slope; no. 7 has a <1% west-facing slope, with hummock/hollow relief exceeding the difference in elevation between the east and west margins of the stand; no. 8 has a 1% west-facing slope, with hummock/hollow microrelief generally less pronounced than that in no. 7.

The internal microtopography indicated by contour maps of the two 5x5 m plots per stand (Figure 13; see section 2.8) ranges from smooth (stand nos. 1 and 2) to hummocky (stands nos. 7 and 8). Stand nos. 3, 4, 5, and to a lesser extent no. 6, have considerable small-scale contour supplied by decaying logs which are now vegetated. Large rocks are not a significant

Figure 12. Computer-drawn topographic contour map of reference stand no. 3. Contour interval is 0.4 m; maximum relief within the stand is ca. 4 m. Except for the shallow depression in the SW quadrant, most of the stand occurs on a SW-facing dune slope. See Methods section 2.8.

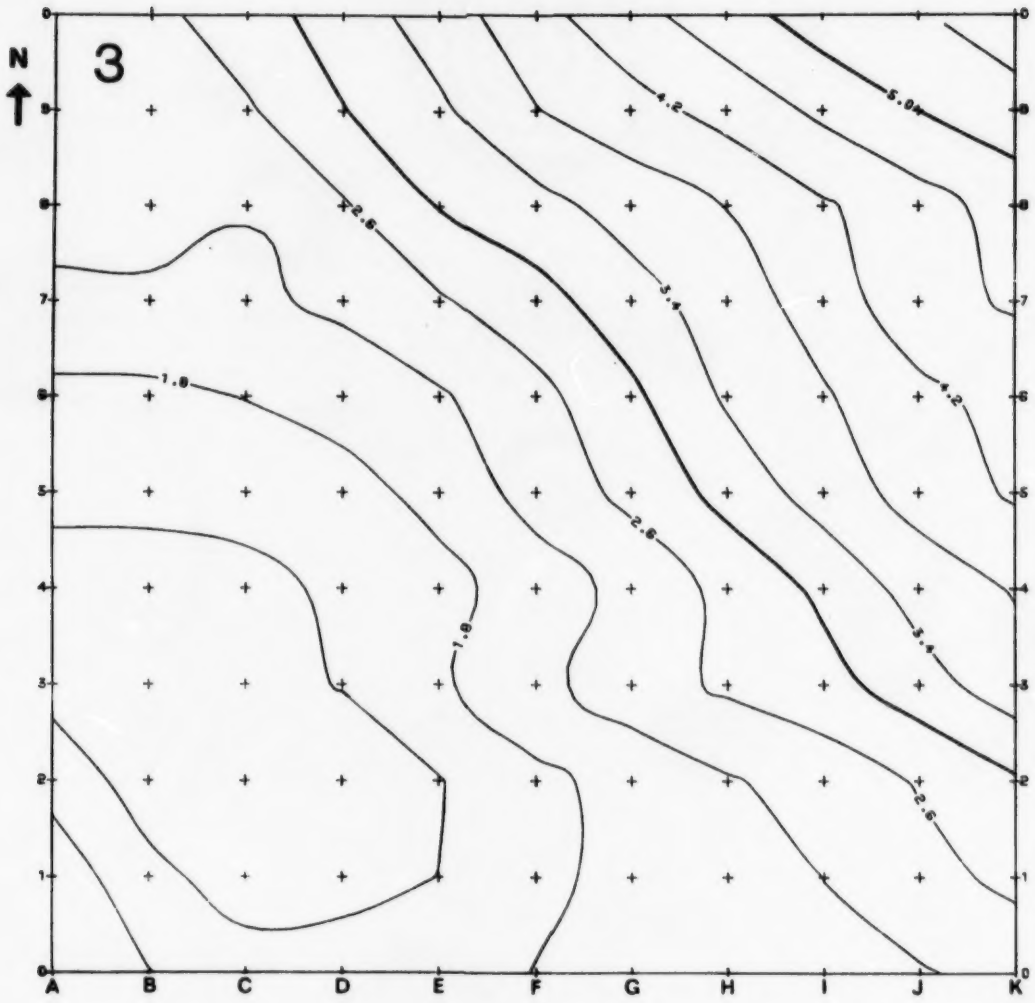
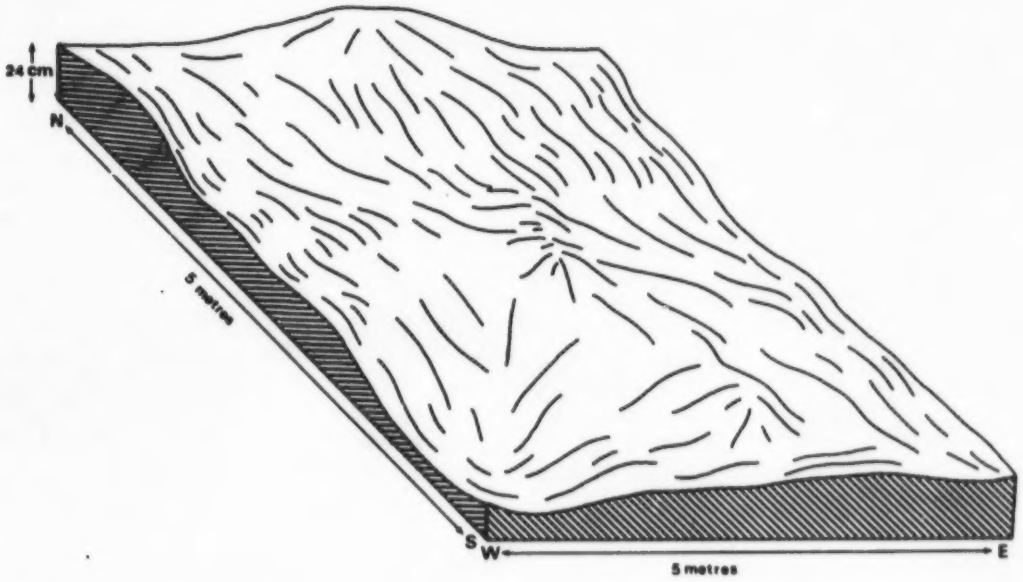
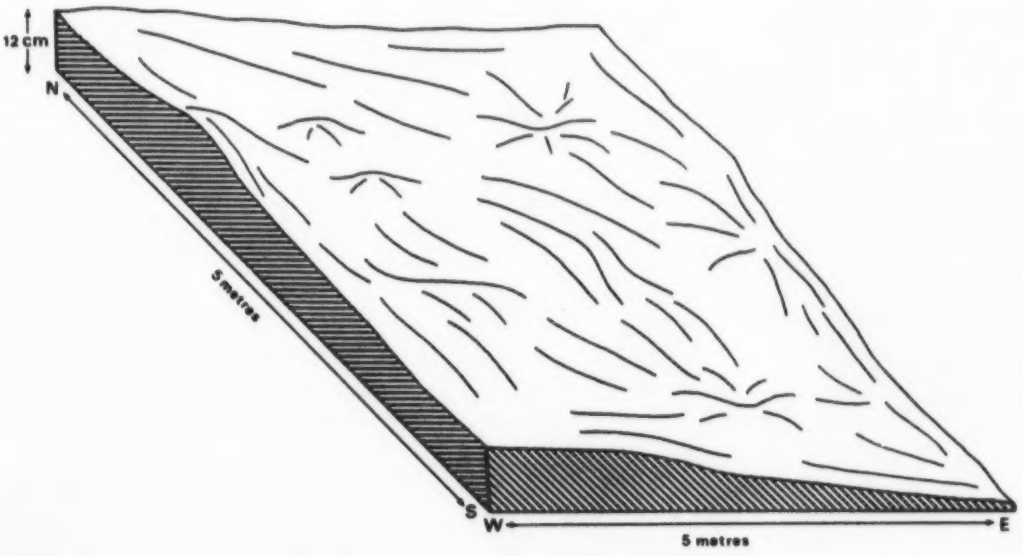

N
3
1.8
2.6
4.2
5.0
5.4
A
B
C
D
E
F
G
H
I
J
K

Figure 13. Micro-relief maps of selected 5x5 m plots in each of the eight reference stands, viewed from a SW perspective. The micro-relief is produced by a combination of mineral soil and organic matter (e.g., logs; see Figure 11) of varying types and stages of decomposition.

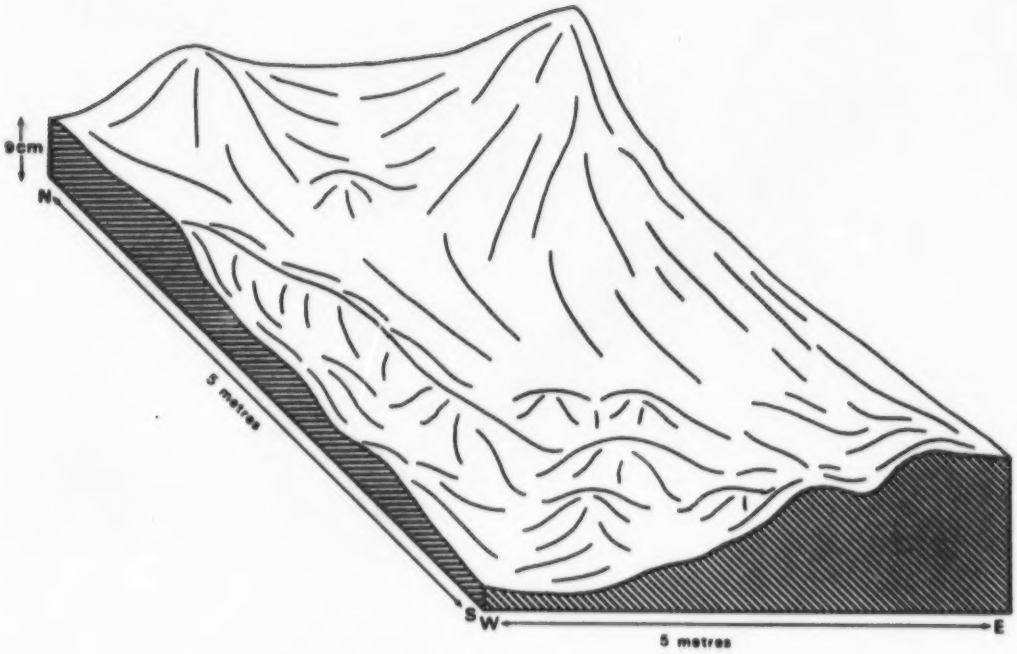
STAND 1 PLOT 8J



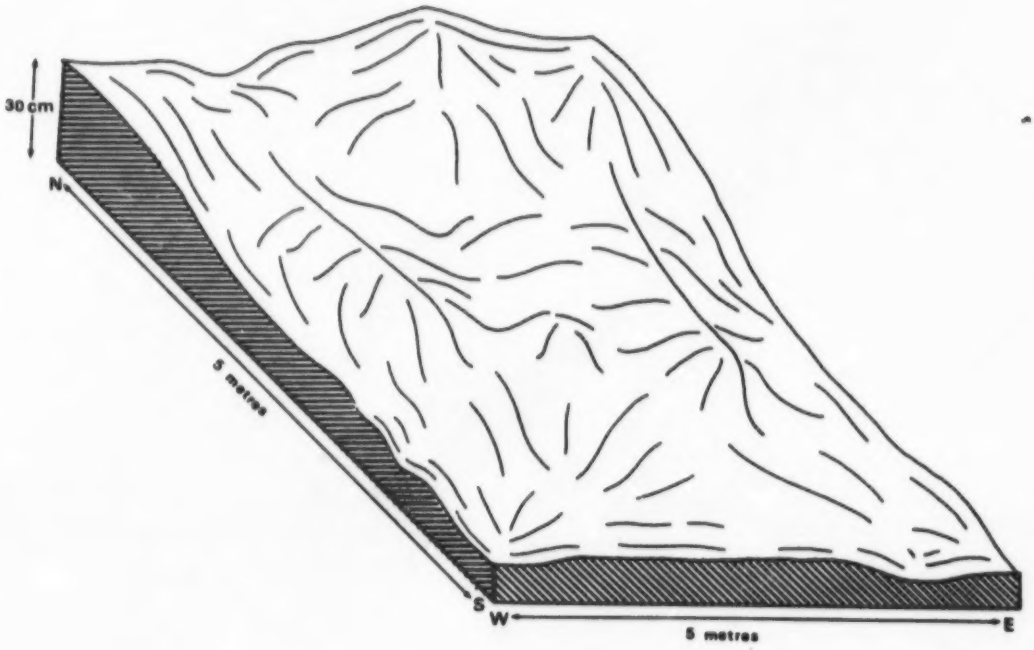
STAND 2 PLOT 2C



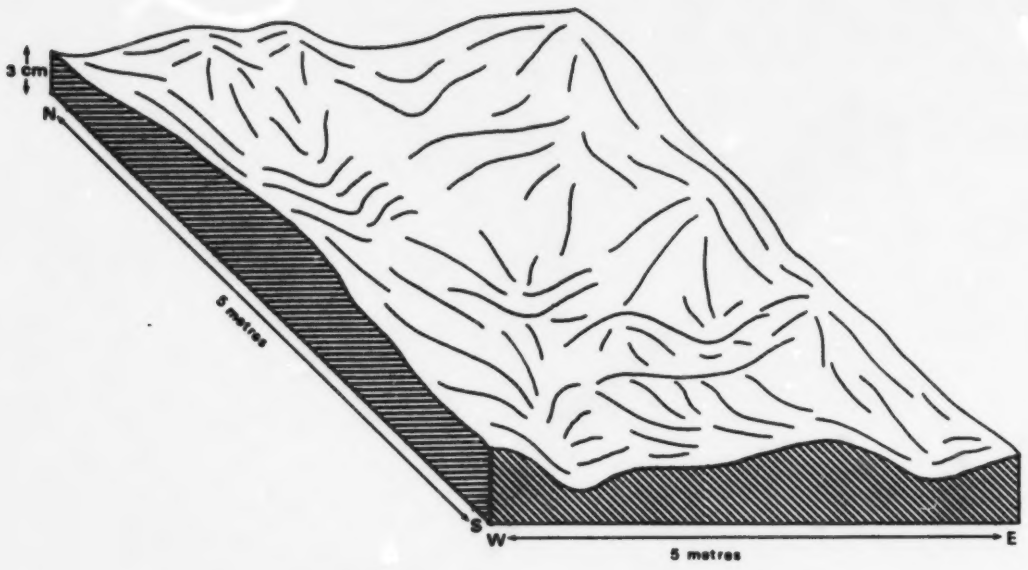
STAND 3 PLOT 6H



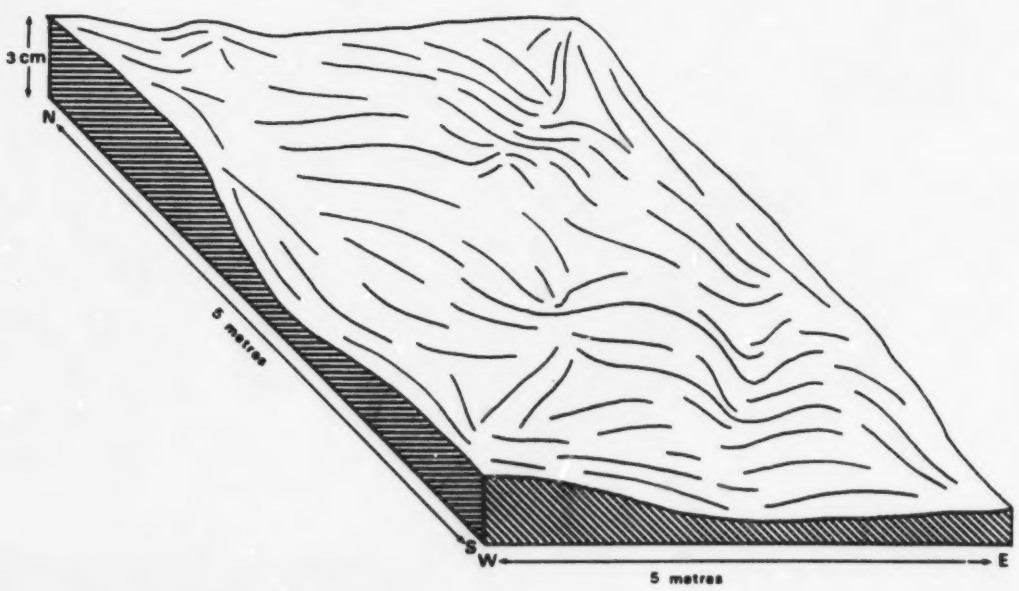
STAND 4 PLOT 4H



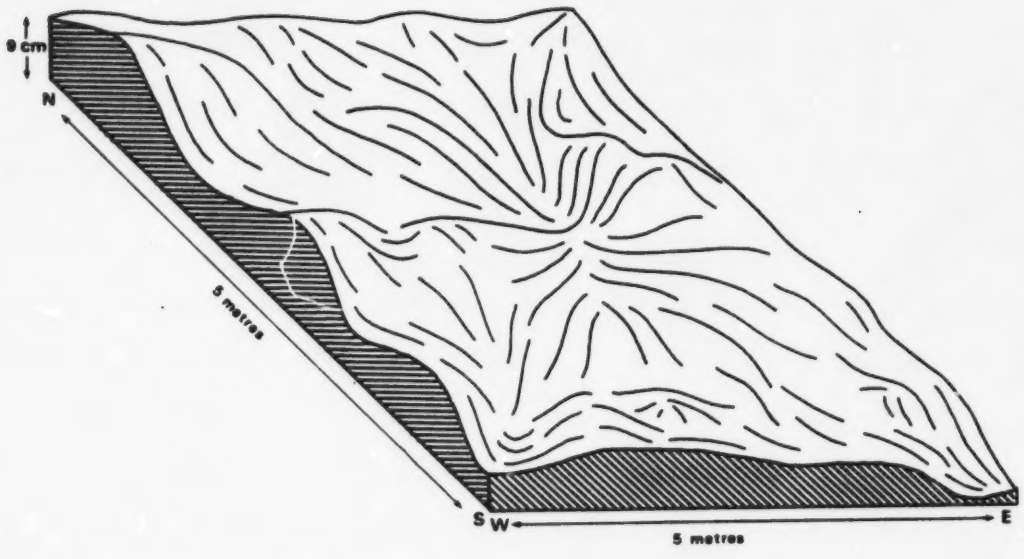
STAND 5 PLOT 2E



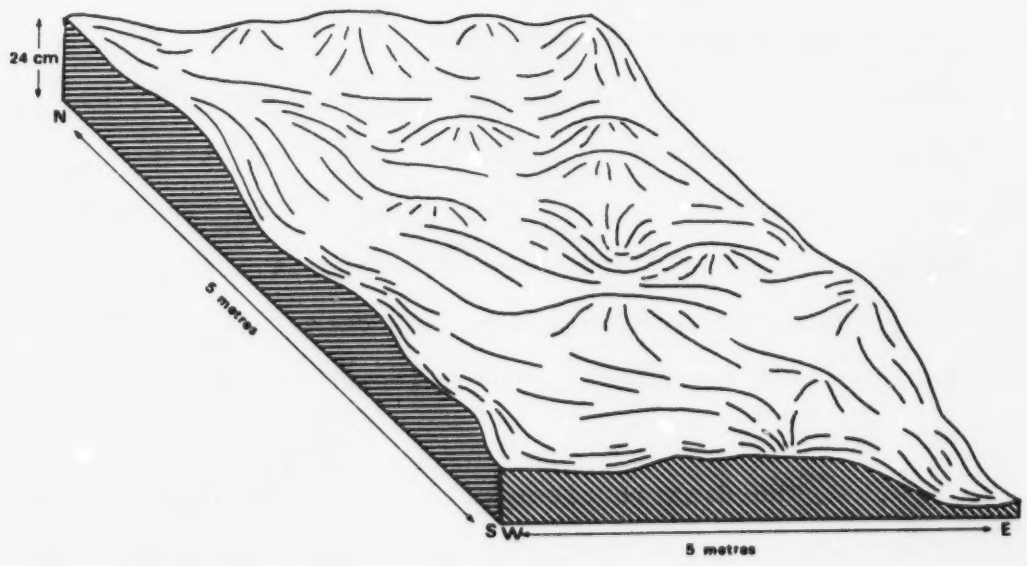
STAND 6 PLOT 4G



STAND 7 PLOT 4E



STAND 8 PLOT 4H



internal feature of the ground surface in this part of the southern boreal forest subzone. The microsites created by organic material of different kinds and decay states in peatlands and mature upland ecosystems provide opportunities for closely neighboring plants to occupy different niches, and may affect species diversity at the stand level or in smaller sampling units.

3.9.1 Vegetation and Topography

Topographic gradients such as the long concave slope of stand no. 3 (Figure 12) or the small-scale mound-and-hollow surface of stand no. 7 (Figure 13) are usually associated with gradients of important plant resources. For instance, a NE-SW gradient of increasing moisture availability might be expected in stand no. 3, accompanied by a shift in plant abundance from relatively xerophytic to more mesophytic species. Or, as in stand no. 7, the plant community of the hummock tops might differ from the one occupying the intervening hollows, perhaps on the basis of differing species' tolerances to poor aeration in the rooting zone. The relationships between topography and vegetation are at least as many as the number of species and stands considered, but we will confine this report to a few selected species in stand nos. 3 and 7.

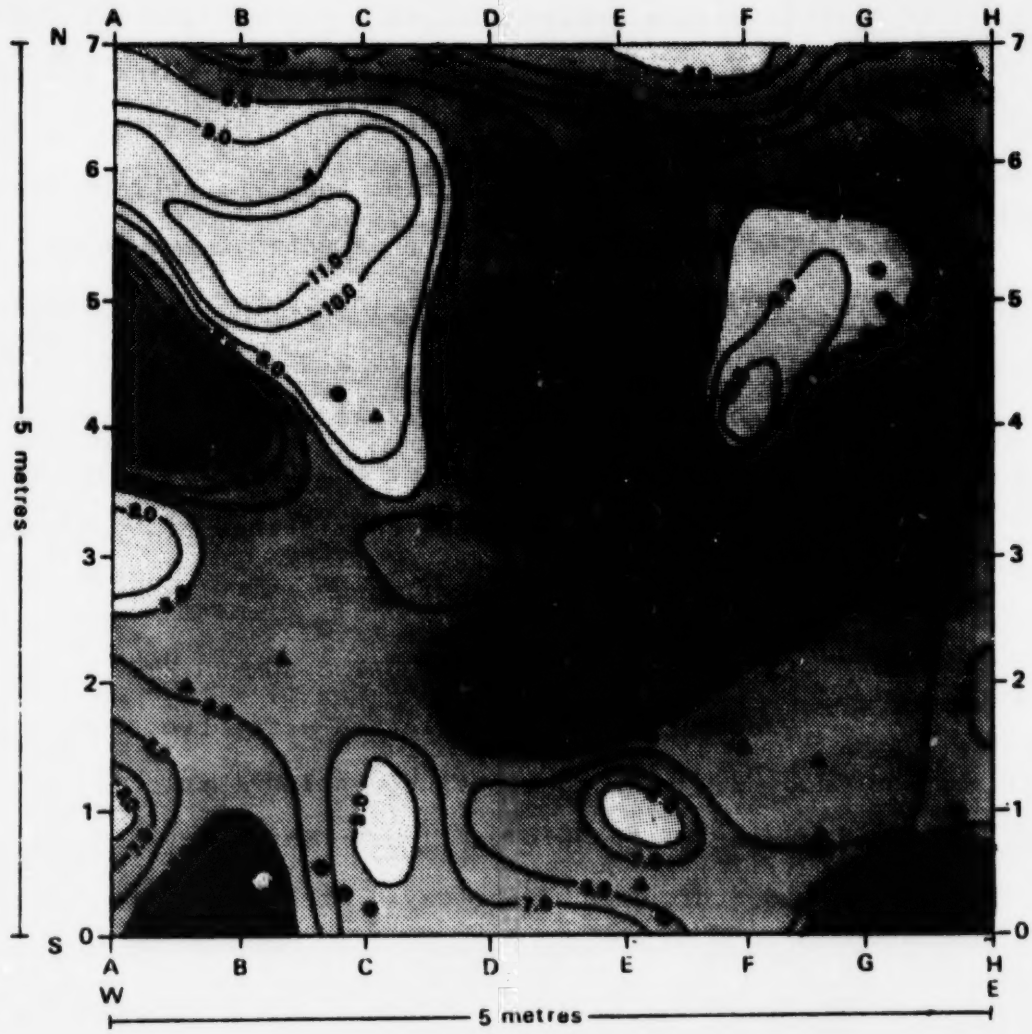
The distributions of July/August cover values of five common species were considered in stand no. 3: *Linnaea borealis*, *Malanthemum canadense*, *Rosa acicularis*,

Rubus idaeus, and *Aralia nudicaulis*. The first three increased in abundance from south to north; *M. canadense* and *R. acicularis* exhibited no quantitative trend in the east-west dimension, while *L. borealis* increased gradually towards the west. *A. nudicaulis* and *R. idaeus* were most abundant in a band near the west boundary of the stand, where slopes are gentle, but were distributed evenly in the north-south direction. Although none of these distributions is perfectly correlated with the NE-SW topographic gradient, the data suggest that (1) *M. canadense* and *R. acicularis* occupy relatively xeric sites within the stand, (2) *A. nudicaulis* and *R. idaeus* inhabit relatively mesic sites, and (3) *L. borealis* is intermediate in habitat preference.

The distribution of *Picea glauca* individuals in stand no. 3 appears to be related to stem size. Stems <2.5 cm DBH are distributed randomly, with 16 of 27 mapped individuals occupying the northeast half of the plot. Larger stems are clumped (21 of the 27; see Figure 10) in the more gently sloping southwest half of the stand. Perhaps site requirements for the initial recruitment of white spruce in jack pine stands are more specific than those for subsequent growth and survival.

Like the species in stand no. 3 discussed above, *Picea mariana* and *Larix laricina* seedlings occupy different but overlapping topographic positions in stand no. 7 (Figure 14). Though both species are found around

Figure 14. Combined micro-contour and vegetation map of 5x5 m plot no. 4E in reference stand no. 7, showing the locations of immature black spruce and larch. Contour interval is 1 cm. See Methods section 2.8.



Picea mariana ●

Larix laricina ▲

the margins of the deeper hollows, *P. mariana* is more common on the hummocks. In a 5x5 m plot in which maximum relief is about 25 cm, the average larch seedling is about 3 cm lower in elevation than the average black spruce. Certainly this is not unexpected, as larch is commonly found closer to the margins of boreal lakes than black spruce. Nevertheless, it is significant that such patterning occurs within as well as between peatland stands. Variability in surficial features in this case appears to contribute to the coexistence of *P. mariana* and *L. laricina*.

3.10 RAINFALL INTERCEPTION DURING SUMMER STORMS

Precipitation was collected after two storms in stand no. 3, with contrasting results (Table 14). The rainfall event of 26 July was low in intensity and evenly distributed throughout the day. Throughfall was 75% of precipitation in the open during this storm. Precipitation collected in no. 3 after the evening thunderstorm of 3 August was apparently 5% greater than that received in the single outside collector, although the 1 mm difference is within the range of expected variability. Further sampling is needed to (1) confirm the relatively high interception by jack pine canopies observed for storms of low intensity, and (2) more carefully measure rainfall amounts falling in open areas outside the stand.

Table 14. Distribution of precipitation received within stand no. 3 during two rainfall events in 1983. See Methods section 2.7.

	July 26	August 3
Precipitation received in the open (mm)	26.0	16.5
Mean precipitation received in stand (mm)	19.4	17.4
Number of collectors in stand[a]	111	116

Percent of precipitation received in open	Number of Collectors	
>155	0	3
145-155	1	2
135-145	0	5
125-135	4	8
115-125	1	16
105-115	4	23
95-105	5	27
85-95	20	14
75-85	24	6
65-75	17	6
55-65	15	3
45-55	6	1
35-45	8	2
<35	6	0

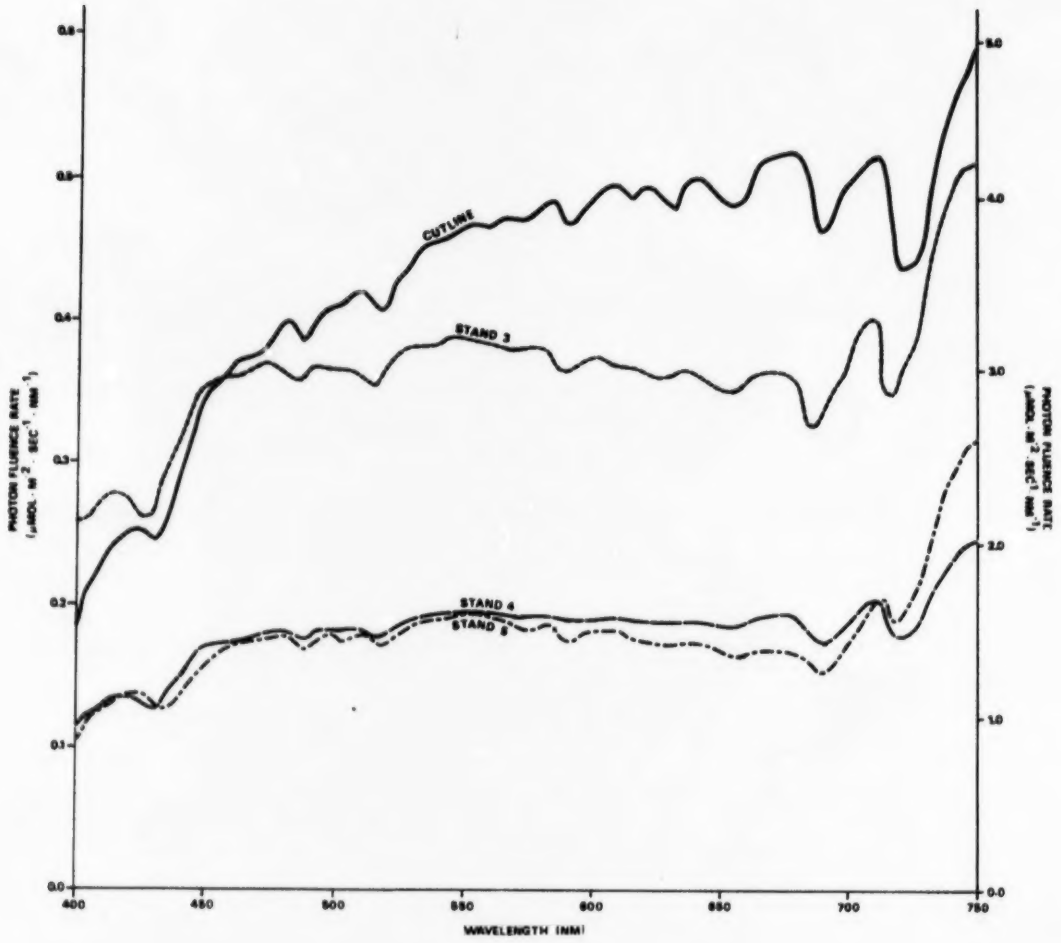
[a] Ten and five cups were overturned or damaged during July 26 and August 3 storms, respectively; the standard number is 121 cups.

Another feature of the precipitation throughfall pattern in stand no. 3 is the high degree of point-to-point variation, despite the relative uniformity of the pine canopy (Table 14). The amount of precipitation reaching the forest floor is potentially a factor affecting the species composition and/or cover and stature of the forest understory. Interception undoubtedly contributes to the xeric microsites and distinctly xerophytic microcommunities typically found at the bases of trees. However, wind speed and direction must also affect the distribution of precipitation; the correlation between precipitation received at the same locations on 26 July and 3 August was very low ($r = +.20$).

3.11 SPECTRAL DYNAMICS OF LIGHT IN THE FOREST INTERIOR

Light is reduced in intensity and altered in spectral distribution in its passage through forest canopies of all types (Figure 15). The light available to understory plants is particularly deficient in the red wavelengths (660 nm), which are absorbed and used in photosynthesis by leaves in the forest overstory. One objective of the preliminary light sampling done in 1983 was to measure the quality and quantity of light reaching the forest floors of the reference stands in late summer compared with that received in unobstructed open areas (see section 2.6).

Figure 15. Light spectra (400-750 nm) in and outside three reference stands during the mid-day period of 2 August 1983. Measurements made with a LICOR spectral radiometer; see Methods section 2.6.


CUTLINE
STAND 3
STAND 4
STAND 5
PHOTON FLUENCE RATE
(μMOL · M⁻² · SEC⁻¹ · nm⁻¹)
WAVELENGTH (NM)
400
450
500
550
600
650
700
750
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
2.0
3.0
4.0
5.0

During the mid-day period of a cloudless day in late August, spectral distributions were obtained for eight randomly located points on the forest floor of four reference stands (nos. 3, 4, 5, 8; Table 15). Light intensity (400-700 nm) was highest beneath the pine canopy of stand no. 3. Except for one high reading from an opening in stand no. 8, the other three stands were about equal in light intensity. There was a large difference in the Zeta ratio (ratio of red:far red light) under the single mixedwood canopy sampled (no. 5: *Populus tremuloides* and *Picea glauca*) compared with those of the three coniferous stands. Comparing the curves for stand nos. 4 and 5 in Figure 15, needle-leaved coniferous trees appear to absorb less red light and absorb more far red light than broad-leaved angiospermous trees. It appears that the fate of a photon of light incident upon a leaf is a species-specific property which may be affected by leaf structure, orientation, and pigmentation.

3.12 SEASONAL DYNAMICS OF THE AVIFAUNA

Tabulations of the avifauna in the eight reference stands during the snow-free season in 1983 followed the same methodology as in 1982. Spring bird migrations in 1983 were 7-10 days earlier than in 1982. This apparently coincided with the earlier snow melt and warmer temperatures in 1983. A combined total of 47 bird species have been recorded in the reference stands during 1982 and 1983.

Table 15. Mean photosynthetic photon flux density (PPFD) and Zeta red/far red ratio under several canopy types in the Hondo - Lesser Slave Lake study area during the mid-day period, 2 August, 1983.

Location	Canopy type	Time (MDT)	PPFD	Zeta ratio
Seismic Line	Open	1217 h	985.8	1.06
Stand 3	Closed jack pine	1402-1424 h	205.9	.84
Stand 4	Closed white spruce	1303-1333 h	53.6	.90
Stand 5	Closed aspen	1141-1212 h	42.9	.58
Stand 8	Closed black spruce	1503-1534 h	108.1	.89

In general, bird diversity increased in most stands in 1983, with the exception of stand no. 3 (Table 16). The largest change occurred in black spruce habitats in stand nos. 7 and 8. In both years the average number of species in all stands peaked in June, with a slight decline in July.

The species composition of bird communities in the eight reference stands during this two-year period suggests certain affinities among stands. Bird frequencies were evaluated in the following ways:

"Constant" - occurring in 7-8 reference stands

"Frequent" - occurring in 4-6 reference stands

"Occasional" - occurring in 1-3 reference stands

In contrast, bird "occupancy" of a particular stand is based on a scale from 1 to 6 monthly occurrences (Tables 17 and 18).

It is notable that 1982 had 4 species not found in 1983, whereas 1983 had 12 species not found in 1982. However, the overall avifaunal similarity of the two years, in terms of bird species composition, was quite high (68% in common).

The oldest stands and mixedwood stands with more available niches tend to have the highest bird diversity. Some species have low frequency but high occupancy, suggesting a relatively narrow range of habitat preference.

Table 16. Numbers of bird species recorded in the eight reference stands of the Hondo - Lesser Slave Lake study area at monthly intervals and during the entire 1982 and 1983 snow-free seasons.

Survey Date[a]		Reference Stand Number								Mean Number Species
		1	2	3	4	5	6	7	8	
May	1982	7	5	4	3	3	3	4	8	4.6
	1983	7	6	5	9	12	10	8	6	7.9
Jun	1982	12	14	10	10	11	16	4	10	10.9
	1983	15	14	11	13	17	9	12	13	14.6
Jul	1982	11	11	8	7	15	12	11	5	10.0
	1983	12	14	8	14	9	13	11	13	11.8
Aug	1982	10	10	8	9	7	5	7	6	7.8
	1983	8	10	4	6	8	8	8	5	7.1
Sep	1982	6	4	6	4	3	6	3	3	4.4
	1983	8	6	1	6	5	6	6	3	5.3
Oct	1982	7	4	1	5	4	3	2	3	3.6
	1983	2	2	3	3	4	7	4	3	3.6
Mean Number	1982	8.8	8.3	6.5	6.7	7.5	6.8	6.2	6.2	
	1983	8.7	8.7	5.4	8.5	9.2	8.8	8.2	7.2	
Total Census	1982	17	16	16	14	19	20	15	14	
	1983	18	18	15	19	22	21	21	21	

[a] Surveys completed during the second week of each month in 1982 and during the first week of each month in 1983.

Table 17. Bird species frequency and occupancy in the eight reference stands of the Hondo - Lesser Slave Lake area based on six monthly surveys during the 1982 snow-free season. Species grouped in order of decreasing frequency, i.e. from eight stands to one.

Bird Species			Stand No.
Common Name	Code Name	Scientific Name*	12345678
Black-capped Chickadee	BCCH	Parus atricapillus	45334216
Pine Siskin	PISI	Carduelis pinus	44225513
Gray Jay	GRJA	Perisoreus canadensis	34223333
Chipping Sparrow	CHSP	Spizella passerina	43322332
Slate-colored Junco	SCJU	Junco hyemalis	23312253
Common Raven	CORA	Corvus corax	24312332
Myrtle Warbler	MYWA	Dendroica petechia	42223321
Red-eyed Vireo	REVI	Vireo olivaceous	22-32122
Yellow Warbler	YEWA	Dendroica coronata	321222-2
Red-breasted Nuthatch	RBNU	Sitta canadensis	--2511-1
Ovenbird	OVEN	Seiurus aurocapillus	222-22--
Hermit Thrush	HETH	Hylocichla gutta	432-2-1-
Ruby-Crowned Kinglet	RCKI	Regulus calendula	112---32
White-throated Sparrow	WTSP	Zonotrichia albicollis	-11-212-
Boreal Chickadee	BOCH	Parus hudsonicus	2-1114--
Golden-Crowned Kinglet	GCKI	Regulus satrapa	--16-3-2
Western Tanager	WETA	Piranga ludocicina	--1112--
Evening Grosbeak	EVGR	*Coccothraustes vespertina	--1-231-
Yellow-bellied Sapsucker	YBSA	Sphyrapicus varius	1--3-2-1
Common Yellowthroat	COYE	Geothylpis trichas	----1211
Common Nighthawk	CONI	Chordeiles minor	22----1-
Swainson's Thrush	SWTH	Hylocichla ustulata	-11--1--
Common (Wilson's) Snipe	COSN	Capella gallinaga	23-----1
Warbling Vireo	WAVI	Vireo gilvus	1--2-1--
American Robin	AMRO	Turdus migratorius	51------
Barn Swallow	BASW	Hirundo rustica	4-----1-
Solitary Vireo	SOVI	Vireo solitarius	---11---
Black-throated Green Warbler	BTGW	Dendroica virens	----11--
White-winged Crossbill	WWCR	Loxia leucoptera	------11

...Continued

Table 17. 1982 Concluded

Bird Species			Stand No.
Common Name	Code Name	Scientific Name*	12345678
Three-toed Woodpecker	TTWO	Picoides tridactylus	-1------
Townsend's Warbler	TOWA	Dendroica townsendi	--2-----
Connecticut Warbler	COWA	Oporonis agilis	----1---
Pileated Woodpecker	PIWO	Dendrocopus pileatus	----1---
Purple Finch	PUFI	Carpoducus paupureus	-----1--
Olive-sided Flycatcher	OSFL	*Contopus borealis	-------1
Brown Creeper	BRCR	*Certhia americana	--------
Yellow-shafted Flicker	YSFL	Colaptes auratus	--------
Spruce Grouse	SPGR	*Dendragapus canadensis	--------
Blue Jay	BLJA	Cyanocitta cristata	--------
Ruby-throated Hummingbird	RTHU	Archilochus colubris	--------
Killdeer	KILL	Charadrus vociferous	--------
American Redstart	AMRE	Setophaga ruticilla	--------
Lincoln's Sparrow	LISP	Melospiza lincolnii	--------
Black-and-white Warbler	BAWW	Mniotilta varia	--------
Chestnut-sided Warbler	CSWA	Dendroica pensylvanica	--------
Palm Warbler	PAWA	Dendroica palmarum	--------
Winter Wren	WIWR	Troglodytes troglodytes	--------

* Scientific names follow THE BIRDS OF CANADA by W. Earl Godfrey (1966) unless changed in the American Ornithologists' Union Check-List (6th edition, 1983), as noted with an asterisk (*).

Table 18. Bird species frequency and occupancy in the eight reference stands of the Hondo - Lesser Slave Lake area based on six monthly surveys during the 1983 snow-free season. Species grouped in order of decreasing frequency, i.e. from eight stands to one.

Bird Species			Stand No.
Common Name	Code Name	Scientific Name*	12345678
Black-capped Chickadee	BCCH	Parus atricapillus	45546634
Gray Jay	GRJA	Perisoreus canadensis	36431444
Slate-colored Junco	SCJU	Junco hyemalis	35443432
Pine Siskin	PISI	Carduelis pinus	23335434
American Robin	AMRO	Turdus migratorius	54411231
Red-eyed Vireo	REVI	Vireo olivaceus	33324321
Myrtle Warbler	MYWA	Dendroica petechia	33233322
Common Raven	CORA	Corvus corax	11142244
Ruby-Crowned Kinglet	RCKI	Regulus calendula	21311233
Boreal Chickadee	BOCH	Parus hudsonicus	2--33113
Common (Wilson's) Snipe	COSN	Capella gallinago	332-1-21
Ovenbird	OVEN	Seiurus aurocapillus	122122--
Hermit Thrush	HETH	Hylocichla guttata	32-121-1
Chipping Sparrow	CHSP	Spizella passerina	21112-2-
Yellow Warbler	YEWA	Dendroica coronata	221-21-1
Yellow-bellied Sapsucker	YBSA	Sphyrapicus varius	--13441-
White-throated Sparrow	WTSP	Zonotrichia albicollis	---21-12
White-winged Crossbill	WWCR	Loxia leucoptera	---211-1
Common Nighthawk	CONI	Chordeiles minor	22----11
Barn Swallow	BASW	Hirundo rustica	432-----
Golden-Crowned Kinglet	GCKI	Regulus satra	---314--
Evening Grosbeak	EVGR	*Coccothraustes vespertina	----111-
Western Tanager	WETA	Piranga ludocicina	---2-1-1
Black-and-white Warbler	BAWW	Mniotilta varia	----111-
Yellow-shafted Flicker	YSFL	Colaptes auratus	11----1-
Red-breasted Nuthatch	RBNU	Sitta canadensis	---6-3--
Blue Jay	BLJA	Cyanocitta cristata	-3-2----
Lincoln's Sparrow	LISP	Melospiza lincolnii	------21
Swainson's Thrush	SWTH	Hylocichla ustulata	------21
Spruce Grouse	SPGR	*Dendragapus canadensis	--1---1-

...continued

Table 18. 1983 Concluded

Bird Species			Stand No.
Common Name	Code Name	Scientific Name*	12345678
Olive-sided Flycatcher	OSFL	*Contopus borealis	1-------
Three-toed Woodpecker	TTWO	Picoides tridactylus	-1------
Palm Warbler	PAWA	Dendroica palmarum	---1----
Brown Creeper	BRCR	Certhia americana	----1---
Connecticut Warbler	COWA	Oporonis agilis	----1---
Common Yellowthroat	COYE	Geothlypis trichas	----1---
Purple Finch	PUFI	Carpodacus purpureus	-----1--
Ruby-throated Hummingbird	RTHU	Archilochus colubris	-----1--
Pileated Woodpecker	PIWO	Dendrocopus pileatus	-----1--
American Redstart	AMRE	Setophaga ruticilla	------1-
Killdeer	KILL	Charadrus vociferous	-------1
Chestnut-sided Warbler	CSWA	Dendroica pensylvanica	-------1
Winter Wren	WIWR	Troglodytes troglodytes	-------1
Solitary Vireo	SOVI	Vireo solitarius	--------
Warbling Vireo	WAVI	Vireo gilvus	--------
Black-throated Green Warbler	BTGW	Dendroica virens	--------
Townsend's Warbler	TOWA	Dendroica townsendi	--------

* Scientific names follow THE BIRDS OF CANADA by W. Earl Godfrey (1966) unless changed in the American Ornithologists' Union Check-List (6th edition, 1983), as noted with an asterisk (*).

Frequency and occupancy values of some individual bird species varied considerably between years. For example, the Chipping Sparrow and Evening Grosbeak were more common in 1982 than in 1983. The Black-capped Chickadee, American Robin, and Red-eyed Vireo had higher frequency values in 1983 than in 1982. Also, some species showed strong habitat preference. For instance, the Red-breasted Nuthatch seems to be an indicator species for mature white spruce stands, whereas the Hermit Thrush and Yellow-shafted Flicker were often prevalent in young, open stands. The White-winged Crossbill has only been recorded in mature black and white spruce habitats where spruce seeds are plentiful.

Compilation of bird song recordings in the eight reference stands continues. An audio library will document bird identification on (1) an individual, bird-specific basis, (2) a community-specific basis, and (3) by habitat type.

Observations of the avifauna in 1982 and 1983 suggest that 1983 was a relatively "normal" year in the southern boreal subzone, since it lacked the pulse of tent caterpillar and associated bird activity that occurred in 1982.

3.13 OBLIQUE COLOR AIRPHOTOGRAPHY OF REFERENCE STANDS AND STUDY AREA

Sections 5.1 and 5.2 of the Appendix include annotated color oblique airphotos of the eight reference

stands and the larger Hondo - Lesser Slave Lake study area taken from a Midwest Bell Jet Ranger helicopter on 29 September 1983 (see section 2.10). The pictures were taken at mid-day from several angles and altitudes just past the time of peak autumn coloration; some are of excellent quality.

4. REFERENCES CITED

Adams, W.P., and D.R. Barr. 1974. Techniques and equipment for the measurement of snow cover, including stratigraphy. Occasional Paper No. 3, Department of Geography, Trent University, Peterborough, Ontario. Pages 11-26.

Busby, J.R. 1976. Energy and water relations of some boreal forest mosses. Ph.D. Thesis, University of Alberta, Edmonton. 179 pp.

Clymo, R.S. 1970. The growth of *Sphagnum*: Methods of measurement. J. Ecol. 58:13-49.

Environment Canada. 1975. Canadian normals, 1941-1970. Volume 1-SI. Temperature; Volume 2-SI. Precipitation. Downsview, Ontario.

Geiger, R. 1965. The climate near the ground. Harvard University Press, Cambridge, Massachusetts.

Johnson, E.A. 1981. Vegetation organization and dynamics of lichen woodland communities in the Northwest Territory, Canada. Ecology 62: 200-215.

La Roi, G.H. 1984. The response of vegetational communities to aerial emissions: permanent sample plots - special winter report. Research Management Division, Alberta Environment. 19 pp.

La Roi, G.H., and M. Ostafichuk. 1982. Structural dynamics of boreal forest ecosystems on three habitat types in the Hondo - Lesser Slave Lake area of north central Alberta in 1981. Research Management Division, Alberta Environment, RMD-80/35A; and Recreation, Parks and Wildlife Foundation. 157 pp. (= "First Report")

La Roi, G.H., M.S. Ross, and M. Ostafichuk. 1983. Structural dynamics of boreal forest ecosystems on three habitat types in the Hondo - Lesser Slave Lake area of north central Alberta in 1982. Research Management Division, Alberta Environment, RMD-80/35A; and Recreation, Parks and Wildlife Foundation. Volume I. 93 pp. (= "Second Report")

Martin, W.L., T.L. Sharik, R.G. Oderwald, and D.W. Smith. 1981. Equations for estimating above-ground phytomass in the understory of Appalachian oak forests. Virginia Polytechnic Institute and State University, School of Forestry and Wildlife

Resources, Publication No. FWS-3-81. Blacksburg, Virginia. 6 pp.

Packer, J.G. 1983. Flora of Alberta. Second edition (first edition by E.H. Moss). University of Toronto Press. 687 pp.

Parmintor, J. 1983. Fire-ecological relationships for the biogeoclimatic zones and subzones of the Fort Nelson Timber Supply Area. Planning, Development, and Research Section, Protection Branch, British Columbia Ministry of Forests, Victoria, B.C. 128 pp.

Pruitt, W.O., Jr. 1958. Qali, a taiga snow formation of ecological importance. Ecology 39: 169-172.

Rowe, J.S. 1979. Concepts of fire effects on plant individuals and species. Contributed paper to: Symposium on fire in northern circumboreal ecosystems. Fredericton, New Brunswick, October 22-24, 1979.

Sampson, R.J. 1978. Surface II graphics system. Revision 1. Kansas Geological Survey, Lawrence, Kansas.

Smith, W.B., and G.J. Brand. 1983. Allometric biomass equations for 98 species of herbs, shrubs, and small trees. U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station, Research Note No. NC-299. 8 pp.

5. APPENDIX

5.1 ANNOTATED LIST OF COLOR SLIDES

The 28 slides listed below are arranged in three groups. The first group (nos. 1 to 15) consists of oblique and near-vertical photos taken from a helicopter (see sections 2.10 and 3.13) on 29 September 1983. XY coordinates of objects on photos are given as percentages of the horizontal (X) and vertical (Y) dimensions of the photos, measured from their lower left corners. The second group (nos. 16 to 27) consists of lateral photos of reference stand nos. 1 and 5 from fixed positions (see Second Report, section 2.6) at six one-month intervals during the 1983 snow-free season. These photos should be compared with those taken from the same two vantage points in 1982 (see Appendix sections 6.2 and 6.3 of the Second Report. Slide no. 28 shows the pollen collecting device installed in reference stands by Dr. Charles Schweger, Department of Anthropology, University of Alberta (see Second Report, section 4.9).

Slide No.	Reference Stand No.	Date	Annotation
1	1	29 Sep	High-altitude oblique view of stand from south. Highway no. 2 and Department of Transportation storage compound on right. SW corner photo target visible at X20Y50 (see coordinates explanation in above paragraph).
2	1	29 Sep	Low-altitude near-vertical view of Pinus banksiana canopy and understory with NE corner target visible at X30Y50.

Annotated List of Color Slides Continued

Slide No.	Reference Stand No.	Date	Annotation
3	2	29 Sep	High-altitude oblique view of stand from NW. Stand located at X35Y65. Highway no. 2, access road to stand, and Department of Transportation compound visible.
4	2	29 Sep	Low-altitude near-vertical view of Pinus banksiana canopy and understory with corner target visible at X60Y70.
5	3	29 Sep	High-altitude oblique view of stand from east. Stand located at X60Y40. Highway no. 2 and Bullet Lake visible. Stand no. 8 is located at X95Y95. Pinus banksiana forest is dark olive green; Picea glauca and P. mariana forests are blue-green.
6	3	29 Sep	Low-altitude near-vertical view of Pinus banksiana canopy with SE corner target visible at X50Y15. Note dead (yellow) pine needles about to be shed.
7	4	29 Sep	High-altitude oblique view of stand from SE. Stand located at X60Y60. Highway no. 2, large borrow pit and well site visible to NW of stand. Selection felling of large Picea glauca has occurred north of the stand.
8	4	29 Sep	Low-altitude near-vertical view of Picea glauca/Abies balsamea canopy with NW corner target visible at X65Y35. Note abundant woody debris and feather mosses on ground beneath canopy.
9	5 & 6	29 Sep	High-altitude oblique view of stand no. 5 at X65Y50 and no. 6 at X30Y50 on opposite sides of burn margin and seismic line. Highway no. 2 visible in background.

Annotated List of Color Slides Continued

Slide No.	Reference Stand No.	Date	Annotation
10	5	29 Sep	Low-altitude oblique view of two--layered Populus tremuloides/--/Picea glauca forest canopy, with white spruce beneath the aspen. Note contrasting leaf abundance and colors of different aspen clones in autumn.
11	6	29 Sep	Low-altitude near-vertical view of Picea glauca/Populus tremuloides forest canopy, with white spruce now taller than the aspen. NW corner target visible at X35Y30.
12	7	29 Sep	High-altitude oblique view of stand from SE. Stand located at X40Y45. Note Highway no. 2 and its bridge across the Athabasca River at top of picture. Picea mariana is blue-green in color; Pinus banksiana is dark olive--green; Larix laricina is yellow--green in autumn before leaf fall.
13	7	29 Sep	Low-altitude near-vertical view of two-layered Larix laricina/-Picea mariana forest canopy, with scattered larch much taller than the abundant black spruce. Note litter trap (50 x 50 cm) at X40Y30 and clumped dispersion of black spruce.
14	8	29 Sep	High-altitude oblique view of stand from NW. Stand located at X50Y60 on peatland adjoining Bullet Lake. Highway no. 2 is visible in background.
15	8	29 Sep	Low-altitude near-vertical view of Picea mariana canopy with NW corner visible at X40Y45. Note cone-filled, club-shaped tops of mature black spruce crowns and two larches (yellow-green) at Y80.

Annotated List of Color Slides Continued

Slide No.	Reference Stand No.	Date	Annotation
16	1	6 May	Lateral view NE-ward from post 0A to post 1B on first survey date in spring of 1983. Compare with slide no. 1 in Second Report, section 6.2.
17	1	5 Jun	Same view in early summer. Cf. slide no. 2, Second Report.
18	1	2 Jul	Same view in mid-summer. Cf. slide no. 3, Second Report.
19	1	3 Aug	Same view in late summer. Cf. slide no. 4, Second Report.
20	1	8 Sep	Same view in early autumn. Cf. slide no. 5, Second Report.
21	1	6 Oct	Same view in late autumn. Cf. slide no. 6, Second Report.
22	5	7 May	Lateral view E-ward from post 6A to post 6B on first survey date in spring of 1983. Compare with slide no. 7 in Second Report, section 6.2.
23	5	4 Jun	Same view in early summer. Cf. slide no. 8 in Second Report.
24	5	1 Jul	Same view in mid-summer. Cf. slide no. 9 in Second Report.
25	5	5 Aug	Same view in late summer. Cf. slide no. 10 in Second Report.
26	5	7 Sep	Same view in early autumn. (Slide incomplete). Cf. slide no. 11 in Second Report.
27	5	5 Oct	Same view in late autumn. Cf. slide no. 12 in Second Report.

Annotated List of Color Slides Concluded

Slide No.	Reference Stand No.	Date	Annotation
28	8	9 Sep	Pollen collection device installed in understory adjoining south margin of stand no. 8. The upper trap collects pollen from air and rainfall; the lower trap collects only airborne pollen. An identical twin trap is located in the overstory canopy.

5.2 COLOR SLIDES

The 28 color slides supplied with the original set of reports are inserted in two clear plastic pages at the end of the report. Copies of these slides may be purchased from the Research Management Division, Alberta Department of the Environment.